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PLIOCENE FLORAS OF CALIFORNIA AND OREGON

RALPH W. CHANEY CARLTON CONDIT
DANIEL I. AXELROD

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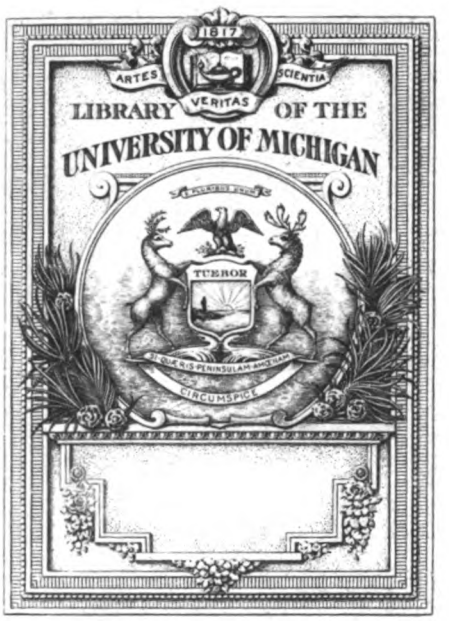

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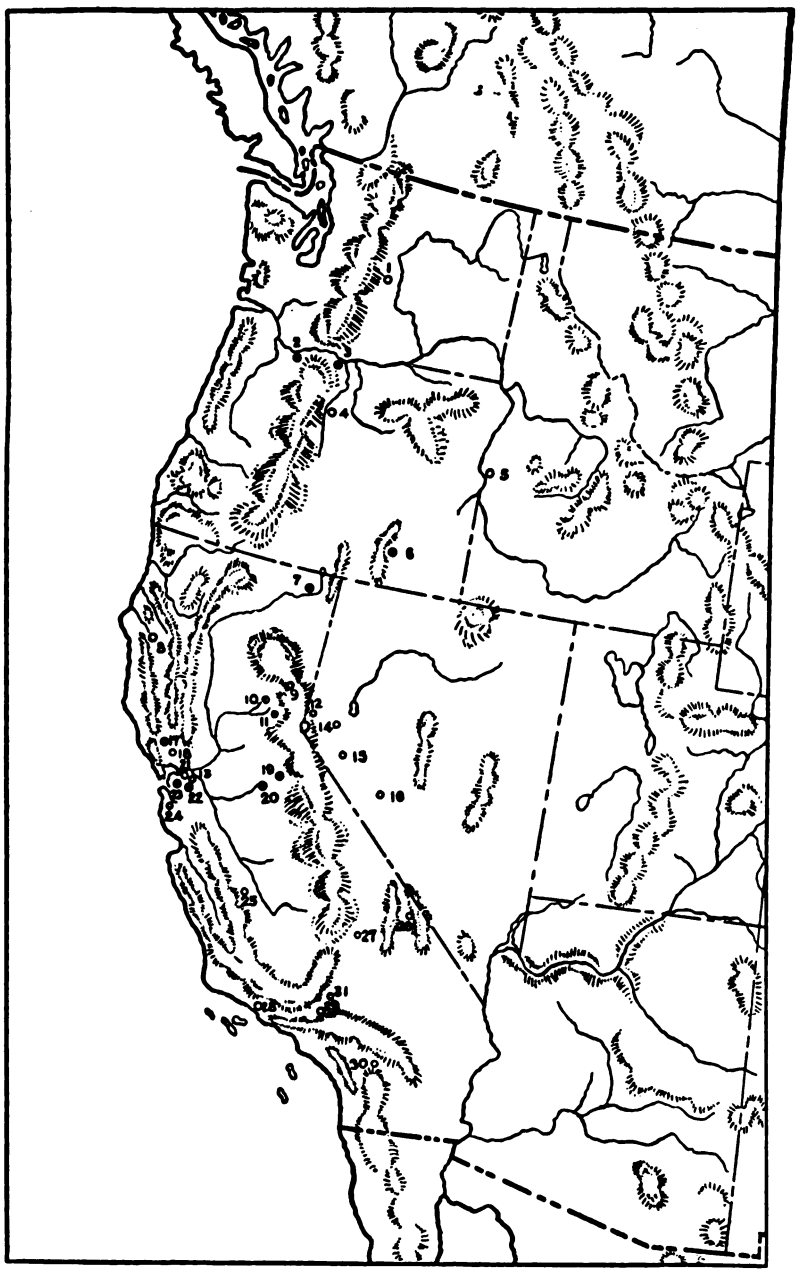

FIG. 1. Mio-Pliocene and Pliocene plant localities in the western United States. (Solid circles indicate floras described in this volume; open circles indicate other floras.)

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CONTRIBUTIONS TO PALEONTOLOGY

PLIOCENE FLORAS OF CALIFORNIA AND OREGON

Edited by
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DANIEL I. AXELROD

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Introduction

RALPH W. CHANEY

In most parts of the northern hemisphere the record of Pliocene vegetation is less completely known than that of older Tertiary horizons. This gap in the sequence of Cenozoic floras has been particularly wide in western North America, where Miocene and older plants are abundantly represented. Our meager knowledge of Pliocene vegetation has been due to several factors, of which the following may be mentioned: (1) Climate and topography were generally less favorable to plant life in the Pliocene than in preceding Tertiary time, with the result that forests were restricted in western North America and elsewhere; (2) relatively low water tables, and reduction in numbers of permanent streams, in response to diminished and seasonally limited precipitation, provided fewer situations in which the remains of plants were buried and preserved in the sedimentary record; (3) Pliocene sediments, at least in the western United States, are relatively coarse, with the result that leaf and fruit impressions are less well preserved than in the shales and volcanic tuffs of the Miocene and Eocene; (4) on the Pacific coast, and in many other parts of the world, the Pliocene epoch was characterized by widespread orogeny, and continental sediments of that age are of comparatively limited occurrence. Investigations of the Tertiary floras in western North America during the past quarter-century have shown that in spite of these factors the record of Pliocene vegetation is sufficiently complete to permit its reconstruction and interpretation.

This volume brings to a conclusion the study of ten floras from Oregon and California. The three Oregon floras were collected many years ago, but only with the accumulation of other later Tertiary floras in the West during the past decade has it been possible to refer them definitely to the Lower Pliocene. More recent work by Condit has provided a basis for assigning two California floras to a position transitional between Miocene and Pliocene. Five other California floras have been revised by Axelrod or are here discussed for the first time; they are referred to various levels in the Pliocene. Before considering these floras, a brief review of previous related studies will be given, together with comments on our methods of approach to the problems of Pliocene vegetation.

History of Pliocene Floral Studies in Western North America

The first mention of Pliocene plants in western North America is the "Notice of a fossil forest in the Tertiary of California" by O. C. Marsh (1871). He describes the occurrence of large silicified trunks in Napa County, and correctly states that no difference is discernible between their wood and that of the living coast redwood, *Sequoia sempervirens*. He adds that the age of the beds in

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which the trunks occur "will probably prove to be Pliocene." Further study of the woods from this locality by Platen (1907) resulted in the description of 3 species of conifer and 3 angiosperms. With the discovery of leaf impressions in these deposits, known as the Sonoma tuffs, Dorf added 9 forms to the flora and confirmed its Pliocene age (1930, pp. 7–13, 37–44).

The earliest detailed discussion of a Pliocene flora in western North America is Lesquereux's "Report on the fossil plants of the auriferous gravel deposits of the Sierra Nevada," published in 1878. Working with little knowledge of western stratigraphy, and with incomplete information regarding the modern vegetation which he used for comparison with plant fossils, Lesquereux achieved a high standard of scholarship in his treatment of this and other Tertiary floras, a standard which, in the opinion of the writer, has not since been surpassed. Fifty-six years ago, when only fragmentary information was available regarding the occurrence of fossil plants, Lesquereux considered the Wilcox flora of Tennessee and Mississippi to be of Pliocene age. When he found species from the Chalk Bluffs locality in the foothills of the Sierra Nevada which were related to those of the Wilcox, it was logical to conclude that the age of the California flora was Pliocene also. This reference was supported by Newberry's suggestion (*in* Whitney, 1865, p. 250) that the flora at Table Mountain was of Pliocene age, and that associated mammalian remains were also indicative of the Pliocene (*ibid.*, pp. 251–252). For many years after Lesquereux's study, the auriferous gravels at Chalk Bluffs and Table Mountain were considered to be of the same age; his conclusion that both floras were Pliocene was wholly consistent with the evidence at that time available.

It has subsequently been shown that not less than six horizons are represented in the auriferous gravels as mentioned by Whitney, and as designated by Lesquereux, Turner (1895*a*),[1] Lindgren (1911), and Knowlton (1911). The oldest of these, represented by the deposits at Chalk Bluffs, Independence Hill, and Buckeye Flat, contains a flora recently monographed by MacGinitie (1941), who considers its age to be Middle Eocene. A flora described by Potbury (1935) from LaPorte is considered to be transitional between the Eocene and the Oligocene. Next in age are the Remington Hill and Table Mountain floras, studied by Condit and presented in chapters 2 and 3 of this volume; they are assigned to a horizon transitional between the Miocene and the Pliocene. Somewhat younger is the Oakdale flora, which is discussed by Axelrod in chapter 6. A small flora from iron-stained gravels near You Bet has never been fully studied, but contains typically Pleistocene fruits referable to *Pinus* and *Arctostaphylos*.

Summarizing the early comments of Lesquereux and Newberry, it is of interest to note that both of them recognized the Pliocene aspect of the Table Mountain flora. Lesquereux even went so far as to suggest, in his preliminary

[1] In this paper, Turner recognizes that the gravels at Chalk Bluffs are older than those of the Intermediate Period, to which he referred the deposits at Table Mountain. He notes that Lesquereux made no distinction in age between the floras from these two localities. Following Knowlton, he refers these floras to the Upper Miocene.

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report to Whitney in 1873 (Lesquereux, 1878*a*, p. 39), that he "considered this group of plants as referable to the oldest Pliocene, or to a formation intermediate between the Miocene and Pliocene"; this is in exact agreement with Condit's conclusion more than fifty years later. Confusion arose, however, from the failure of older paleobotanists to recognize that the Table Mountain flora did not occur in beds of the same age as the Chalk Bluffs flora; neither Lesquereux nor Newberry visited the area, and the error is readily understandable. Turner and Lindgren also failed to differentiate the two deposits clearly as to age. Knowlton's reference of the combined flora to the Miocene may have been in part an effort to average the discrepancies in age between them. It should be mentioned that both Knowlton (1911, p. 61) and Lesquereux (1888, p. 28) suggested that a small flora from near Susanville was possibly as old as Upper Eocene; Knowlton says, "The matrix of the Susanville forms is entirely different from that carrying plants at all other localities, and I think it has yet to be demonstrated that this horizon is not lower and older than the true auriferous gravels." But he did not recognize that the Chalk Bluffs flora also was more ancient than the Table Mountain, and that it was made up of many forms whose modern equivalents live in subtropical regions, whereas the Table Mountain flora is typically temperate. Only with the recent study of the Chalk Bluffs flora by MacGinitie and the conclusion of Condit's investigations here reported have these two floras been adequately distinguished. The accuracy of Lesquereux's original age determination of the Table Mountain flora as oldest Pliocene or Mio-Pliocene seems now well established.

During several decades following Lesquereux's auriferous gravels paper, there were only casual references to Pliocene plants in the western United States. Remains of grass were noted by Lesquereux in beds of doubtful Pliocene age at Clear Lake, California (1887). Turner quotes Knowlton regarding the occurrence of *Sequoia* wood in fragmental andesite considered to be of Pliocene age, south of Cammel Peak, Bidwell Bar atlas sheet, California (1895*b*, p. 408). A pine cone from the valley of the Snake River, Idaho, was described by Knowlton as coming from Pliocene lake beds (1901). He also described a new species of *Woodwardia* from the Cascades of the Columbia, at first considering its age Pleistocene (1910), and later Pliocene (1919, p. 809). The writer has had several opportunities to examine the rather large collection of which this fern is a part, made near Cascade Locks by G. K. Gilbert, and believes it is definitely referable to the Eagle Creek formation, now considered to be of Lower Miocene age. Hannibal's paper "A Pliocene flora from the Coast Ranges of California" represents a substantial contribution to our knowledge of later Tertiary vegetation (1911). He describes the occurrence of 20 forms, based on leaves and fruits, assigning them to modern species. He concludes that the Santa Clara formation in which they occur is of Upper Pliocene age. Subsequent studies in this area, near the coast of central California, have confirmed this age reference.

The preceding paragraphs summarize the information regarding Pliocene vegetation that was available when our program of paleobotanical investigation was inaugurated in the western United States in 1916.

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A few years later, leaf impressions were discovered in the Sonoma tuff at several localities. In the early twenties, Alexander and Kellogg made a small but important collection from beds of Pliocene age near Alturas. In addition, they cooperated with the writer in the collection of fossil wood from the Ricardo formation of southern California. Occasional specimens of well preserved leaves were brought in by students of the departments of Paleontology and Geology at the University of California, mostly from deposits in the San Francisco Bay area. All this material was given preliminary consideration in the writer's first statement regarding the sequence and interpretation of the Tertiary floral units of western North America (Chaney, 1925*b*, pp. 32–35).

In 1927 Dorf began his investigation of the Pliocene floras of California. These centered in the Coast Ranges of west-central California, and included the Sonoma and Santa Clara floras, several newly discovered floras located as far north as Humboldt County and southward to the vicinity of Santa Barbara, and also the material from Alturas, in northeastern California (Dorf, 1930). At the same time Webber had under way her study of the wood from the Ricardo formation of southern California (1933).

The extensive collecting program organized by Frick in southern California yielded a Pliocene flora of great value during the early thirties. The collector, Guy Hazen, later obtained additional material and cooperated fully with us when, through the courtesy of Mr. Frick, this flora from the Mount Eden beds was turned over to Axelrod for study. A preliminary paper (Axelrod, 1934) was followed by his systematic study and analysis of the Mount Eden flora (1937). Using the field technique developed during this piece of work, Axelrod has subsequently collected floras of Pliocene and Miocene age from some forty localities in California and Nevada under the auspices of the Carnegie Institution of Washington and the Geological Society of America, and more recently with the support of a fellowship granted by the National Research Council. Nine papers have been published, and are listed in the bibliography. In the present volume he has completed the revision of the Sonoma, Orinda (Mulholland), and Alturas floras, using large collections which have accumulated since the floras were studied by Dorf. In addition he has described two newly discovered floras, also of Pliocene age, from central California, and has discussed the Alvord Creek flora from southeastern Oregon.

Condit's interest in later Tertiary floras began some years ago when he was a student at the University of California. In his paper on the Neroly flora (1938), he presents evidence regarding its composition and environment; he concludes that it represents an Upper Miocene horizon, but considers the possibility that it is transitional between the Miocene and the Pliocene. On the basis of a comparison with the Remington Hill and Table Mountain floras, found across the Great Valley from the Neroly, on the lower slopes of the Sierra Nevada, we are inclined toward the view that all three of these floras may best be interpreted as transitional. The reader is referred to chapters 2 and 3 of this volume for discussion of these age considerations by Condit.

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Another flora intermediate in age between the Miocene and Pliocene has been described by Dorf from the Lower Idaho formation in the Snake River basin of southwestern Idaho (1936). The survival of numerous Miocene species in this flora is suggestive of uppermost Miocene age, whereas stratigraphic relationships and associated vertebrate remains favor its reference to the lowermost Pliocene. A somewhat younger flora from the Columbia Plateau has been described by Chaney from the Deschutes formation of eastern Oregon (1938*a*). The absence of all typical Miocene species from the Deschutes flora, and its strictly riparian and rather meager aspect, have been interpreted as indicating Pliocene age. This flora is discussed below in relation to other Pliocene floras from Oregon, and evidence is presented favoring its reference to the Middle Pliocene. Elsewhere in the Columbia Plateau, our knowledge of the terrestrial life of the Pliocene has been largely limited to the mammalian fauna of the Rattlesnake formation of the John Day Basin (Merriam, Stock, and Moody, 1925). It seems probable that the Deschutes formation represents an equivalent of the Rattlesnake, which accumulated at a higher elevation where the climate was better suited to arborescent vegetation.

More than twenty-five years ago, the writer made small collections of plants from volcanic sediments overlying the Columbia River basalt, and situated on opposite sides of the Cascade Range in northern Oregon. From one of these localities, near The Dalles, Thomas Condon had collected a small flora some fifty years before. Neither the Dalles flora nor the Troutdale flora to the west has ever been described, although various references have been made to them, as noted below. In the concluding chapters of this volume, evidence is presented for the reference of these floras to the Pliocene.

Within the past decade, active field work by members of the staff of the National Geological Survey of China has resulted in discovery of the first known floras of Miocene and Pliocene age in China. Discussion of these floras in relation to the vegetation of corresponding age in western North America will be included in the final chapter. They are mentioned here to emphasize the value of a broad geographic viewpoint in the study of such a major problem as the development of vegetation. The relationships of the floras on opposite sides of the Pacific have been sufficiently well established to indicate that wide-reaching rather than local factors have been involved in the later Tertiary history of western North America.

Recognizing the desirability of publishing and coordinating the evidence regarding later Tertiary floras which has been accumulated during the past several decades, the Geological Society of America made a grant in 1939 to enable the writer and his associates to complete their Pliocene studies. Acknowledgment is hereby made to the Geological Society for this generous assistance, and to the Carnegie Institution of Washington for its continued support of the program of studies in Tertiary paleobotany in western North America. Acknowledgment will be given in the chapters which follow to the individuals who have assisted in the collection of specimens and in their interpretation.

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Terminology Applied to Vegetational Units of the Tertiary

There is some ambiguity in the use of the term "flora" with reference to fossil vegetation. In the terminology here employed, a *flora* is a unit of past vegetation from a definite stratigraphic horizon and geographic area, which is sufficiently well represented in the fossil record to have geological or botanical significance. A *florule* is the material from a single locality, and this term is used only when a flora has been collected from more than one locality. In addition, we refer to larger units of vegetation from the standpoint of their centers of origin; such a unit as the Arcto-Tertiary or the Madro-Tertiary (Sierra Madrean) is termed a *Flora,* since it represents a group of plants which maintained its integrity over wide ranges of space and time. Thus we speak of the Arcto-Tertiary Flora, the Troutdale flora which has been largely derived from it, and the Buck Creek florule which represents one of the localities from which the Troutdale flora has been collected. The Arcto-Tertiary Flora had its origin in the north, was dominant over the northern hemisphere throughout most of Tertiary time, and is still represented in restricted form in the forests of North America and Eurasia. It is the equivalent of the major unit of vegetation which has been termed the Turgayan flora by Kryshtofovich (1935, p. 339). The Troutdale flora includes the group of plants which are known to have lived in the lower Willamette Valley of Oregon during Lower Pliocene time. The Buck Creek florule comprises the collection made from rocks of Troutdale age in the valley of Buck Creek.

During the early years of our study of Tertiary paleobotany in the western United States, the close similarity of certain fossil floras to living forests became apparent. In our first discussions of the Bridge Creek and Mascall floras (Chaney, 1924, p. 144; 1925*a*, pp. 12–17; 1927, pp. 73–77, 80–83), relationships to the modern redwood forest, to the border-redwood forest, and to deciduous forests in eastern North America and Eurasia were pointed out. Subsequently we have regularly made reference to groups of fossil species whose equivalents have survived in modern forests, terming them the Redwood Element, the Deciduous Element, or the Asiatic Element of the flora involved. These relationships between Recent and Tertiary plants provide a graphic means of comparing known forests with those indicated by the fossil record. Interpretation of Tertiary floras in terms of earth history depends largely on such comparisons with modern forests whose climatic and topographic requirements may be accurately measured.

In later years, elements in Tertiary floras have been designated by several workers in western North America, but the application of names has not always been consistent. It seems desirable at this time to standardize the use of the terms applied, and to clarify the implications of such usage.[2] Following consultation with Herbert L. Mason, Lincoln Constance, and Daniel I. Axelrod, all of whom have spent much time considering the problem, definitions and a

[2] The reader is referred to chapter 11 of Wulff's *Historical plant geography* for a discussion of floral elements in modern vegetation.

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classification have been devised. A fossil flora may be broken down into elements whose living equivalent species are found in association at the present time. An *element* may be defined as a group of fossil plants whose modern related species occupy a major geographic and climatic province. It is essentially the equivalent of the plant formation as defined by Weaver and Clements (1929, p. 43), or of the climax community. The application of the terms "plant formation" and "climax community" to modern vegetation may not always be sufficiently exact to warrant their close comparison with elements of Tertiary vegetation.

In all Tertiary floras studied, divergent types of vegetation may be noted which are assignable to several elements. The five elements commonly recognized in Tertiary floras of western North America are:

1. *The West American Element,* made up largely of conifers, with broad-leafed evergreens commonly present. The region which their most typical living equivalents now occupy is characterized by temperate climate, with winter rainfall and summer drought, and with a moderate range of temperature.

2. *The East American Element,* made up largely of broad-leafed deciduous genera, with conifers of minor importance. The region on the eastern side of North America now occupied by their living equivalents is characterized by temperate climate, with well distributed rainfall of which a considerable amount comes during the summer, and with seasonal extremes of temperature, most trees losing their leaves during the cold season.

3. *The East Asian Element,* made up largely of genera now confined to eastern Asia, and including also genera occurring in other parts of the world. The climatic requirements of the living equivalents of this element are essentially the same as those outlined for the equivalents of the East American Element, except that the East Asian Element also includes genera which now range into the tropics.

4. *The Southwest American Element,* made up largely of microphyllous plants whose living equivalents have their centers of distribution in the mountains of northern Mexico, and extend northward into New Mexico and Arizona and along the coast from Cape San Lucas to central California and into the interior. Seasonal extremes both of temperature and of precipitation characterize these regions, in which the climate is temperate except at the south.

5. *The Caribbean Element,* made up mostly of evergreen angiosperms with large, entire-margined, thick leaves. The region occupied by the modern equivalents of Tertiary members of this element, including southern Mexico, Central America, northern South America, and the West Indies, has a subtropical to tropical climate, with high, generally well distributed rainfall and temperatures free from frost.

The Caribbean Element in the Tertiary of western North America is best developed in floras of Eocene and Lower Oligocene age; it survived, however, into the Miocene of Washington and Oregon in coastal and other favorable situations, and has been noted with greatly reduced representation in Pliocene floras as far north as central California. The West American Element is dominant in Upper Oligocene and Miocene floras of the western United States, continuing into the Pliocene and down to the present at middle latitudes and in the mountains farther south. The East American and East Asian Elements

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are also abundantly represented in floras of Middle Tertiary age, becoming rare in the Pliocene and disappearing at the close of that epoch. The Southwest American Element makes its first well established appearance in the Miocene of southern California, although there is reason to believe that it may have been represented in the Florissant flora of Colorado, which MacGinitie considers to be of Oligocene age. It ranged northward into Oregon and Idaho at the close

FIG. 2. Distribution of modern vegetation corresponding to Tertiary floral elements in North America.

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of the Miocene, and was partly restricted southward during the Pliocene. In the floral chapters and conclusion of this report, the time-space relationships of these elements in the Pliocene and related floras of western North America will be considered in detail.

Reference to the classification presented in table 1 may raise the question why an Interior American Element has not been designated to cover the grass-

TABLE 1

ELEMENTS AND COMPONENTS IN THE TERTIARY FLORAS OF WESTERN NORTH AMERICA

West American Element
- Redwood Component
- Border-redwood Component
- North-coast coniferous Component
- Sierra-Cascade Component
- Rocky Mountain Component

East American Element
- Beech-maple Component
- Oak-hickory Component
- Coastal pine Component
- Swamp cypress Component

East Asian Element
- Northern temperate highland Component
- Northern temperate lowland Component

East Asian Element—*continued*
- Southern temperate highland Component
- Southern subtropical lowland Component
- Southern tropical lowland Component

Southwest American Element
- Conifer woodland Component
- Oak woodland Component
- Chaparral Component
- Closed-cone pine Component
- Coastal sage Component

Caribbean Element
- Warm-temperate highland Component
- Subtropical lowland Component
- Tropical lowland Component

land climax of the Great Plains. A complete enumeration of modern plant climaxes in North America must of course include this grassland unit. Since our classification refers not to modern but to Tertiary vegetation, and since few fossil collections from the western United States include representation of the grassland climax, we have not designated an element corresponding to it. The important studies of fossil grasses by Elias (1932, 1935) may at some future time warrant the inclusion of an Interior American Element made up of Tertiary grasses and forbs. In the same way, it may eventually be desirable to set up a Boreal American Element to include Tertiary plants whose modern equivalents are now most characteristic of high North American latitudes. Such plants appear to make up an important part of several older Tertiary floras from the arctic islands, but since they are not well represented in the fossil floras of Oregon and adjacent areas, the Boreal American Element is not included in the classification here presented.

From even a cursory reference to the distribution of tree genera in modern forests, it is apparent that there must be some overlapping of the constituents of the elements as defined. Though the East American and East Asian Elements each contain distinctive genera, they have other genera in common, with species whose living equivalents occur in both hemispheres. The marked similarity of the vegetation on the east sides of the two continents has been well known since the days of Asa Gray, and is to be expected because of the climatic similarity of the regions. But there are also differences, which are emphasized by the study of forest evolution in the western United States; it

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therefore seems essential that separate element rank be assigned to these major forest units of the two continents. There are likewise close relationships between the East and West American Elements; it is not clear, for example, whether the fossil sycamore *Platanus dissecta* Lesquereux has as its modern equivalent the eastern species *P. occidentalis* Linnaeus, or the western species *P. racemosa* Nuttall; one of the most common Middle Tertiary species of black oak, *Quercus pseudo-lyrata* Lesquereux, seems almost equally related to living oaks on both sides of the continent. Such dual assignment of fossil species is to be expected in a classification as general as ours, and serves to emphasize the common origin of forests now widely separated, though once intermingled in the generalized vegetation of the Tertiary period in the western United States.

A further comment seems necessary to clarify our attitude toward comparisons between fossil and modern plants. All our lists of equivalent living species are at best a tentative expression of opinion regarding the modern affinities of fossil species. These suggested relationships are based largely on leaf similarities, with the supporting evidence of fruits or seeds also available in many cases. Such comparisons are highly suggestive, and are made whenever the fossil specimens are sufficiently well preserved; but they are not to be considered as final evidence of phylogenetic relationships. Whether a fossil oak finds its nearest living descendant in the forests of North America or in those of eastern Asia, the fact that living equivalents may be noted on both continents is highly significant in any consideration of the Tertiary history of vegetation in the northern hemisphere. Such relationships also make possible a more natural interpretation of the origins of modern forests.

Each of the elements designated in Tertiary floras may be further subdivided into *components* which represent their major floristic units. These correspond roughly to the associations of modern forests (Weaver and Clements, 1929, pp. 45–48, 425–426). Component names are assigned to emphasize dominant plants, secondary topographic features, or climatic zones. The components most commonly recognized in discussing the Tertiary history of the West American Element are the Redwood, the Border-redwood, the North-coast coniferous, the Sierra-Cascade, and the Rocky Mountain. Usage will vary somewhat until the significance of these components in Tertiary vegetation becomes better understood. The Border-redwood Component may represent an ecotone between the Redwood Component and two components of the Southwest American Element, the Oak woodland and the Chaparral. Locally the modern forest equivalents of the North-coast coniferous and the Sierra-Cascade Components grade into each other, and their place as distinct units in the forests of the Tertiary may in some cases be open to question.

A natural division of the East American Element will recognize the Beech-maple, the Oak-hickory, the Coastal pine, and the Swamp cypress Components. All these except the Coastal pine are well represented in the Middle Tertiary floras of the western United States. It is possible that additional components may be designated as current studies of the Mascall and Bridge Creek floras of Oregon are continued.

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The East Asian Element is here classified largely on the basis of climatic and topographic units. It seems probable that future field studies in Asia will make possible floristic names corresponding to those assigned to the components of the East American Element, names which will carry a more significant connotation than those of table 1.

The Southwest American Element is divisible into the above-mentioned Oak woodland and Chaparral Components, and also into Conifer woodland, Closed-cone pine, and Coastal sage. The Oak woodland Component, occurring under a wide range of topographic and climatic conditions, represents a more diverse floral unit than the other components of the Southwest American Element; but it does not appear to indicate a wider range of composition than certain components in the East American and West American Elements.

The subdivisions of the Caribbean Element, like those of the East Asian, are tentative as here presented. This element is only slightly involved in the discussion of later Tertiary floras in the present volume, and such more definite component names as seem necessary will be assigned later in papers concerned with Eocene floras.

It should be emphasized that element and component names are applied to groups of fossil plants to emphasize their resemblance to modern vegetation, and that they do not necessarily coincide with the names of units involved in the study of living plants. In cases where groups of fossil plants have living equivalents occupying well defined geographic or climatic provinces and subprovinces, it is convenient to designate them in terms of these living equivalents and their habitats. Our element and component names indicate the *present* distribution of surviving equivalents of Tertiary species, not their *past* distribution; there is no inherent basis for assuming that a Miocene oak assigned to the East American Element was living in the eastern United States during that epoch; only its discovery there in Miocene rocks would indicate that its range at that time coincided with its present distribution. Further, there is not the slightest implication that the provinces covered by element names represent the centers of dispersal of the plants involved. The modern occurrence of *Cercidiphyllum* is no more an indication that it had its origin in China than is the presence of *Sequoia* in California evidence that it is a native son. Centers of origin and modern range of species may in some cases coincide; but when there is a wide time discrepancy between living trees and their fossil equivalents, there is likely also to be a wide discrepancy between their Tertiary and Recent distribution, representing the distances covered in the course of forest migrations through geologic time.

One further consideration warrants brief comment at this point. Many floras, especially those of Middle Tertiary age, include several elements representing forests now widely separated in regions with diversified climates. We conclude that such vegetation was of a more generalized type than most living forests. Physical changes toward the later part of the Tertiary period brought diversified topography and climate, producing the geographic and climatic provinces which we recognize, each with its distinctive forest. Differentiation

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of the generalized vegetation of the past into modern floristic units may best be expressed by the recognition of diverse ingredients in Tertiary forests. Such ingredients, which we term elements and components, represent groups of trees whose varying response to earth change has resulted in their present restriction to the regions best suited to their requirements. A survey of modern forest environments, and a comparison of their vegetation with that of the past, provides the most adequate basis for an understanding of continental history, since it makes possible a reconstruction of the topographic and climatic setting of Tertiary forests.

Taxonomic Principles Involved in the Study of Pliocene Floras

Not only generalized forests but generalized species were living in western North America during the Tertiary period. Some of these, which would be termed plastic if they were living plants, show evidence of subsequent differentiation which is comparable in extent to the diversification of Tertiary floras into the modern forests of the northern hemisphere. Just as the Arcto-Tertiary Flora has been so altered that its coniferous members (West American Element) survive largely in the western United States, and its angiosperm members (East American and East Asian Elements) are for the most part restricted to the eastern sides of the northern continents, so in the case of certain Tertiary white oaks there has been a tendency toward differentiation into numerous modern species with ranges now widely separated geographically.

The Eagle Creek flora, from the Lower Miocene of the gorge of the Columbia River, includes two species of white oak, *Quercus bretzi* and *Q. columbiana* (Chaney, 1920, pp. 170–171). Numerous well preserved leaves of these oaks have recently been collected by Wilder from a near-by locality on the west side of the Cascades, and will be discussed in his forthcoming paper on the Molalla flora. *Quercus bretzi,* whose leaves are large and commonly characterized by compound lobes, is recorded in the Middle Miocene Latah flora of Washington (Brown, 1937*b,* p. 508), and lasted on with somewhat smaller leaves into the Upper Miocene in the Thorn Creek flora of Idaho (Smith, 1941, p. 510). An undescribed related form, with still smaller leaves and deeper lobes, is found in the later Miocene Mascall flora of Oregon, and survives in a flora recently collected by the writer at Satus Pass, Washington, in beds which appear to be referable to the Ellensburg formation, of Lower Pliocene age. This deep-lobed species seems to be the immediate ancestor of the living *Q. garryana* Douglas, now largely confined to coastward slopes in the Pacific states but locally extending east of the mountains. The older *Q. bretzi,* with larger, shallow-lobed leaves, shows a marked resemblance to such living compound-lobed oaks as *Q. alba* Linnaeus, *Q. macrocarpa* Michaux*,[3] and *Q. stellata* Wangenheim of the eastern United States; no typically compound-lobed oaks are known to occur in eastern Asia, although the simple-lobed *Q. mongolica* Fischer and

[3] In this discussion, species marked with an asterisk (*) have leaves most similar to the fossil specimens.

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Q. liaotungensis Koidzumi occasionally have leaves with lobes resembling those of *Q. bretzi.*

The other Lower Miocene white oak, *Q. columbiana,* whose leaf margins are characterized by simple lobes, continued into the Middle Miocene Latah (Brown, 1937*b,* pp. 508–509), into the later Miocene Mascall flora, and into the Upper Miocene Thorn Creek flora (Smith, 1941). Leaves figured by Smith as *Q. payettensis* Knowlton (*ibid.,* pl. 9, figs. 2, 6) seem indistinguishable from smaller leaves of *Q. columbiana,* as do her figures of *Q. boisiensis* H. V. Smith (*ibid.,* pl. 10, figs. 1, 8). In these younger floras the leaves are not only smaller but fewer than in the Lower Miocene, with *Q. pseudo-lyrata* and other black oaks becoming increasingly numerous. A slightly smaller and more slender white oak is *Q. mccanni* Berry from the Latah flora, probably also represented in our collections from the Mascall. This species may not be separable from *Q. columbiana.*

Leaves closely related to *Q. columbiana* and *Q. mccanni,* but averaging much smaller, are recorded in this volume from the Mio-Pliocene Remington Hill flora of the west-central slopes of the Sierra Nevada, and from the Lower Pliocene Dalles and Troutdale floras of northern Oregon. In order to emphasize their reduced size, they are herein described as a new species, *Q. winstanleyi.* Leaves of similar size and shape are occasionally found on the living *Q. douglasii* Hooker and Arnott, an abundant oak of the Coast Ranges and westward Sierran slopes of California, but are not typical for that species. Much more similar to the fossil leaves of *Q. winstanleyi* and of the larger *Q. columbiana* are leaves of several modern species in the eastern United States, *Q. bicolor* Willdenow, *Q. muhlenbergii* Engelmann, and *Q. prinus* Linnaeus*; in Europe, *Q. sessiliflora* Salisbury; and in eastern Asia, *Q. aliena* Blume, *Q. fabri* Hance*, and *Q. mongolica* Fischer. Highly suggestive relationships may also be noted between these fossil oaks and such hybrids as *Q. alba* × *muhlenbergii* (California Academy of Sciences Herbarium sheet 83808) and *Q. alba* × *prinus* (University of California Herbarium sheet 119171) from the eastern United States.

The Tertiary white oaks of western North America, and their relationships to living species in the northern hemisphere, are a striking illustration of gradual speciation through geologic time. The writer recently had an opportunity to discuss the history and relationships of American white oaks with Dr. Jesse More Greenman, who stated his opinion that many of them are still in a plastic state, and that their ultimate differentiation into well defined species is yet to be achieved. Trelease has expressed a similar opinion in his discussion of the evolution of the oaks (1924, p. 33). Surely the intergrading leaf types of certain modern species on the borders of their ranges, and their ability to hybridize (Trelease, 1924, pp. 13–17; Small, 1933, pp. 424–431) and produce leaves of intermediate aspect, support the idea that evolution of the oaks must continue still farther before the systematic botanist can speak with confidence of distinct specific entities. Reference to the synonymies recorded by Sargent

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(1922, pp. 304–306), Small (*op. cit.*, pp. 425–426), and Trelease (*op. cit.*, pp. 109–111) gives some idea of the difficulties these men found in their treatment of the living species of the Prinoideae. The paleobotanist is subjected to an even greater handicap when he attempts to assign his oak specimens to well defined species. Seldom with more than leaf impressions at his disposal,[4] he has a problem whose time limits are extended through tens of millions of years. The resemblance of these specimens to the leaves of numerous widely distributed living species, many of whose characters intergrade, and the ability of these modern related species to hybridize and produce polymorphic leaves closely resembling the fossils, must serve to postpone a complete understanding of their relationships until larger collections of fossil specimens have been compared with greater numbers of modern leaves from wide areas and varying habitats. Even then the paleobotanist may have to await, with the botanist, the slow passage of time until the extinction of intermediate living forms shall have resulted in separation of the white oaks into taxonomic units which can be readily distinguished on the basis of their leaves and other characters. In the meantime he may on occasion be forced to adopt an arbitrary attitude toward the specific differentiation of fossil oaks, an attitude justifiable only if he includes with his systematic descriptions a discussion of possible relationships to all similar oaks, both fossil and living.

Recent discussion of this problem with the writer's colleagues Ernest B. Babcock and G. Ledyard Stebbins has indicated that variability in leaf form of Tertiary white oaks is consistent with the genetic make-up of modern members of the genus *Quercus*. Most widespread living plant species are heterogenic and include great numbers of biotypes which may be grouped into more or less distinct ecotypes. In the case of living oaks, the factor of ready interpollination by wind tends to accentuate their heterozygosity, and great genetic variability is the result. The wide range in leaf form of fossil white oaks may be interpreted as indicating that heterozygosity has been a characteristic of the genus *Quercus* from the Tertiary period down to the present. If at some future time extinction shall have reduced both the number of its species and the extent of their distribution, we may anticipate that the surviving homogenic oaks will present fewer problems to the paleobotanist. Thus the opinion of the geneticist is added to that of the systematist and the paleobotanist, and all share the problem raised by the polymorphic character of leaves of the genus *Quercus*.

The taxonomic study of Tertiary vegetation may involve other difficulties not commonly met in modern botany, or in the consideration of Mesozoic and Paleozoic plants, most of which are unlike those now living. In cases where several Tertiary species of different age show relationships to a modern species, it may be difficult to establish natural breaks along the continuity of their phylogeny. Theoretically at least, there may have been tree species which survived several epochs of the Tertiary with changes so gradual that specific

[4] Determinable fruiting structures of *Quercus* are rare in the Tertiary record, and wood specimens so far studied do not provide a basis for specific determination.

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limits cannot readily be established on the basis of the material available for study. If in such cases we had a series of fruits and stems in addition to leaves, it seems probable that modification of at least one of these structures might serve as a basis for specific separation. When only leaves are available in the fossil record, the possibility of establishing such limits is greatly reduced. Just as geologic time must in some cases be arbitrarily subdivided for convenience in discussing the sequence of events in earth history, so it may be necessary to impose limiting names on a relatively unbroken line of plants which has survived, though incompletely recorded, through millions of years down to the present.

A case in point is the Pliocene elm which is widespread from Oregon to central California. Several modern species of the genus *Ulmus* show a wide range of leaf variation which makes their recognition on the basis of foliar structures extremely difficult. One of these, the white elm, *U. americana* Linnaeus, is widely distributed in the eastern United States. It reaches its best growth in the more humid parts of its range, where it occupies flood plains and valley slopes; here the trees are tall, with mature leaves reaching a length of 10 to 15 centimeters and a width about half as great. Westward in the Great Plains this species is largely confined to stream borders, where its height is much reduced and its leaves become progressively smaller. In spite of these geographic differences, the white elm constitutes a readily recognizable species, since there are regional intergradations in size of stem and leaf, and since the fruits and stem structures are essentially constant throughout. But if this species were represented by material as incomplete as the record of its Tertiary equivalents—if, in other words, there were only available for study leaves from several discontinuous areas—it seems probable that botanists might recognize more than one species of elm on the basis of regional leaf variation. At this point in our discussion, the modern taxonomist may interpose the comment that no competent botanist would attempt to establish either differences or resemblances on such scanty material. From his standpoint, it is true that systematic treatment based solely on leaves provides an inadequate basis for taxonomic conclusions, when the auxiliary data of reproductive and vascular structures are available. But if living plants furnished only leaves for study, the student of modern plants would long since have recognized and systematized foliar characters for the determination of species. He would, in fact, have come to know as much about leaf characters as does the paleobotanist. Admittedly he might have fallen into error in referring to more than one species the leaves of white elms from Pennsylvania and Nebraska; but to facilitate his study and interpretation of this scanty body of data, he would have profited by recognizing in some concrete way the differences between the large-leafed and the small-leafed elms from east to west. The paleobotanist regularly finds himself in the situation of this hypothetically handicapped botanist, with the added difficulty that his material shows variation and intergradation not only through space but through time as well. Thus he may need to resort to arbitrary areal or

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stratigraphic distinctions for the sake of establishing the sequence of development of generic lines, or determining their environmental significance upon a changing earth.

Turning to the Tertiary record of the ancestors of *Ulmus americana,* leaves of *U. speciosa,* originally described by Newberry from the Bridge Creek shales of the John Day Basin, are widely distributed in deposits of Upper Oligocene to Upper Miocene age in Oregon, Washington, and Idaho. The average length of 32 specimens available for measurement[5] is 8.9 centimeters; their average width is 4.6 centimeters, or approximately one-half their length; more than half of them have well marked asymmetry at the base, and only a few lack some degree of asymmetry. These Middle Tertiary leaves correspond in size to those of *U. americana* from the eastern part of its range. Here the rainfall is on the order of that indicated by such other members of the Oligocene and Miocene floras as *Sequoia langsdorfii, Alnus carpinoides, Carpinus grandis,* and *Fagus pacifica.* We conclude that the Middle Tertiary equivalent of the American elm had the same favorable habitat and showed the same foliar response as *Ulmus americana* in the eastern United States.

Leaves of elm from transitional Mio-Pliocene and Lower Pliocene beds of California have been referred to another species, *U. californica,* by Lesquereux (1878*a,* pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. 7*a*). He suggested a resemblance to the living *U. alata* Michaux, but comparison with *U. americana* seems more appropriate. These fossil leaves differ from *U. speciosa* in their smaller size; 26 specimens[6] have an average length of 5 centimeters and width of 2.8 centimeters; they are somewhat broader than the leaves of *U. speciosa,* and differ further in having nearly symmetrical bases in a majority of cases. Though these distinctions may be readily noted in most specimens, there are leaves of *U. californica* from the Lower Pliocene of California which are indistinguishable from the smaller leaves of *U. speciosa* from the Columbia Plateau.

Recent collections from the Middle Pliocene of California include 10 specimens of elm leaves which average only 3.7 centimeters in length and 2 centimeters in width.[7] Like leaves of *U. californica,* they are broader and more symmetrical than those of *U. speciosa.* These have been assigned to a distinct species, *U. moragensis,* by Axelrod, who finds that they show a resemblance both to the modern *U. pumila* Linnaeus of eastern Asia and to *U. americana.* They can be readily matched with leaves of the living *U. americana* from regions where the amount of summer rainfall is limited; trees of white elm planted in Berkeley have many leaves of this size and shape. Thus the Tertiary record includes three fossil species which resemble the living white elm, but which differ in size and shape, showing a trend toward smaller size and

[5] Seven specimens from John Day formation (Bridge Creek shales), 1 from Eagle Creek, 1 from Latah, 2 from Upper Cedarville, 21 from Mascall.

[6] Ten specimens from Remington Hill, 10 from Table Mountain, 6 from Black Hawk Ranch.

[7] Five specimens from the Petaluma formation, 1 from the Alturas, 4 from the Lafayette Dam locality of the Tassajero formation.

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broader form from Middle to Upper Tertiary time. It may be suggested that this trend is related to the climatic changes which have characterized western North America since the Miocene. These involve not only lessened annual rainfall, but also its marked reduction during the summer. The sequence from the large-leafed *U. speciosa* of the Miocene to the medium-leafed *U. californica* of the Mio-Pliocene and to the small-leafed *U. moragensis* of the Middle Pliocene seems to be an expression of progressively less favorable climate for the genus *Ulmus,* which resulted in its extinction in western North America at the end of the Pliocene.

Leaves of *Ulmus* in the Dalles and Troutdale floras of Oregon are of the intermediate size which we should refer to *U. californica.* The average length of 17 specimens is 5.9 centimeters, and their average width is 3 centimeters. The larger leaves are well within the size range of *U. speciosa,* although none in our collections are so large as the largest specimens of this Miocene species. It is significant to note that the Troutdale leaves average much larger than those of the Dalles flora, a reflection of more humid conditions at their coastward-slope locality. Taken by themselves, these larger leaves from the Pliocene of Oregon might be confused with the leaves from the older floras. But considering also the smaller leaves which occur with them in greater numbers, they may be interpreted as representing an intermediate stage in the history of *Ulmus* in western North America. By assigning the Dalles and Troutdale leaves to *U. californica,* we not only point out their similarity in size and shape to elm leaves from the Mio-Pliocene and Lower Pliocene of California, but emphasize the changing environment on the western borders of the continent from Miocene to Pliocene time. For additional discussion of this taxonomic procedure involving the designation of what may be called "ecologic" species, the reader is referred to the writer's treatment of the poplars and cherries of the Deschutes and related older floras of Oregon (1938*a,* pp. 212–215), and to the discussion of *Quercus winstanleyi* in chapter 12 of this volume.

Outline of the Floras Included in This Volume

In the chapters which follow, ten floras of later Tertiary age are discussed. Their geographic occurrence, age, and composition are here summarized:

Chapter 2. Remington Hill flora

Western slope of the central Sierra Nevada, about 10 miles east of Nevada City, Nevada County, California.

Age transitional between the Miocene and Pliocene.

Thirty-three species, including 3 gymnosperms (1 indeterminate) and 30 angiosperms. Nine species are described as new.

A total of 1477 specimens are included in our collections.

Chapter 3. Table Mountain flora

Lower foothills of central Sierra Nevada, about 5 miles northwest of Sonora, Tuolumne County, California.

Age transitional between the Miocene and Pliocene.

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Thirty species, including 1 gymnosperm and 29 angiosperms. Six new species are described.

A total of 1085 specimens are included in our collections.

Chapter 4. Black Hawk Ranch flora

Southwestern flank of Mount Diablo, Contra Costa County, east of San Francisco Bay, California.

Age Lower Pliocene.

Eight species of angiosperms.

A total of 200 specimens are included in our collections.

Chapter 5. Mulholland flora

Eastern Oakland-Berkeley hills, 2 miles northwest of Moraga, Contra Costa County, California.

Age Middle Pliocene.

Forty-three species of angiosperms, of which 10 are new.

A total of 2200 specimens are included in our collections.

Chapter 6. Oakdale flora

Lower foothills of the central Sierra Nevada, about 7 miles east of Oakdale, Stanislaus County, California.

Age Middle Pliocene.

Sixteen species of angiosperms, of which 2 are new.

A total of about 200 specimens are included in our collections.

Chapter 7. Sonoma flora

Several localities near Santa Rosa, north of San Francisco Bay, Sonoma County, west-central California.

Age Upper Pliocene.

Forty-four species, including 1 pteridophyte, 6 conifers, and 37 angiosperms. Nine new species are described.

A total of slightly over 600 specimens are included in our collections.

Chapter 9. Alvord Creek flora

Eastern base of Steens Mountain, west of Alvord Ranch, southeastern Oregon.

Age Lower Pliocene.

Twenty-six species, including 8 gymnosperms and 18 angiosperms. Nine new species are described.

A total of about 500 specimens are included in our collections.

Chapter 10. Alturas flora

Rattlesnake Butte, 10 miles west of Alturas, Modoc County, California.

Age Middle Pliocene.

Seven species of angiosperms, 2 of which are given new names.

A total of 70 specimens are included in our collections.

Chapter 11. Dalles flora

Columbia River Gorge, on the east slope of the Cascade Range, near The Dalles, northern Oregon.

Age Lower Pliocene.

Twelve species of angiosperms, of which 2 are new.

A total of 193 specimens are included in our collections.

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Chapter 12. Troutdale flora

Sandy River Valley, on the west slope of the Cascade Range, Multnomah County, northern Oregon.

Age Lower Pliocene.

Nineteen species, including 3 gymnosperms and 16 angiosperms. Six new species are described.

A total of 1046 specimens are included in our collections.

In these ten floras a total of 146 species has been recorded, as listed in table 33. Omitted from table 33 are the following 7 species which are represented by material so inadequate that their inclusion in that list would be of no significance.

Abies ? sp. Condit	Remington Hill
Cyperacites sp. Chaney	Troutdale
Phyllites plinerva Chaney	Troutdale
Poacites sp. Axelrod	Mulholland
Potamogeton sp. Axelrod	Alvord Creek
Prunus sp. Chaney	Dalles
Typha lesquereuxi Cockerell	Mulholland

Fifty-three species have been described as new. The geographic occurrence of these and other Pliocene and Mio-Pliocene floras in western North America is shown on figure 1 (frontispiece).

It is readily apparent that conclusions based on a flora such as the Mulholland, represented by 2200 specimens, are much more likely to be sound than those based on such small floras as the Alturas and Dalles. If larger collections of these latter are subsequently made, there is a strong probability that our ideas regarding their composition, physical indications, or age may be altered. As previously stated, Pliocene formations in western North America rarely contain as many well preserved plant fossils as do those of the Miocene or Eocene. The material on which the following chapters are based is the product of years or even decades of field work. The description and interpretation of these collections therefore provides a summation of our knowledge of Pliocene continental history in Oregon and California.

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2

The Remington Hill Flora

CARLTON CONDIT

Introduction

The Remington Hill flora occurs in fluviatile sediments which have been exposed, largely through gold-mining activities, on the coastward slope of the central Sierra Nevada. These beds, which are essentially the equivalent of the Mehrten formation, were deposited at a considerable elevation above sea level at the end of the Miocene or in earliest Pliocene time. The Remington Hill flora represents upland vegetation which is essentially contemporaneous with the Neroly flora (Condit, 1938) from a lowland coastal habitat in the San Francisco Bay area, and with the Table Mountain flora, discussed in chapter 3.

Acknowledgments are due to Dr. H. L. Mason for many suggestions in making identifications; and to Dr. B. L. Clark and Dr. C. A. Anderson for geologic information and advice. Mr. Clarence Martz, of Nevada City, first brought the Remington Hill locality to my attention, and gave valuable assistance in the field; other field assistance was contributed by Fletcher Pomeroy and Richard W. Chaney.

Geologic Occurrence

The majority of the fossils discussed in this report were collected at Remington Hill, Nevada County, California. Remington Hill lies on the western slope of the central Sierra Nevada at an altitude of 3840 feet in Sec. 1, T. 16 N., R. 10 E., Mount Diablo Baseline and Meridian, Colfax Quadrangle. It is on the southeast side of Chalk Bluffs Ridge, about 10 miles east of Nevada City, and is designated in the University of California collections as locality P3935. (See plate 1.) Approximately 125 specimens were obtained in 1930 by R. W. Chaney at Oakvale Mine, a small drift mine ½ mile southwest of Remington Hill. Oakvale Mine has been abandoned for at least ten years, and collecting there is no longer feasible. Since both field evidence and the fossil assemblages indicate that the collections represent the same vegetation, they will be treated here as a unit. The Oakvale Mine locality will be designated as University of California locality 204. The Sierra Nevada in this region consists of a series of long, gently sloping, flat-topped ridges and deeply incised canyons trending in a general west-southwest direction. At higher elevations to the east the range becomes more rugged and the topography less regular; lower down, the ridges pass into a series of low discontinuous hills which merge into the Great Valley floor, lying less than 100 feet above sea level. All streams drain into the Great Valley and thence into the Pacific Ocean.

The Remington Hill placer mine is excavated in one of the Tertiary channels

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exposed by the canyon of Steep Hollow Creek. The workings have been carried down to bedrock (here a highly altered schist) and have left a vertical face between 50 and 75 feet high. Fossil leaves were collected from beds near the northeast end of the cut, where the vertical section is as follows:

	Thickness in feet
6. Red soil	3
5. Yellow sandy clay, indistinctly bedded	20
4. Gray sandy clay, evenly bedded, bearing fossil leaves in the lower part	5
3. Gray finely banded clay, bearing fossil leaves throughout	7
2. Gray tuffaceous sandy clay, bearing fossil leaves in thickly matted thin layers	1
1. Yellow gravel and sand, indistinctly bedded	6
Talus	17
Total	59

According to Clarence Martz, who has operated the mine, the talus covers approximately 8 feet of coarse gravel, resting directly on bedrock. Above this gravel are about 8 feet of bluish-yellow clay containing no fossil leaves. Overlying the clay, 2 feet of finer yellowish gravels are considered to represent the lower part of member 1 in the section given above. Judging from the debris on the floor of the mine, the lower gravels contain a high proportion of large, moderately well rounded boulders almost wholly quartzose in composition. On the hillside above the face of the placer, occasional outcrops of clay, tuff, and sand were noted for a vertical distance of 100 feet. At that elevation exposures of andesitic tuff-breccia become common, and they are abundant to the top of the ridge, a vertical distance of 400 to 500 feet. All the beds above the schist are essentially horizontal, dipping at most 1° to 3° toward the southwest. Individual members can be traced horizontally for only a short distance, frequently lensing into others. Contacts between beds of different grain size may be sharply defined or gradational, with cross-bedding rare. A sample of the matrix from Oakvale Mine, which appears to be identical with that at Remington Hill, has been studied by Albert L. Repecka, of the Department of Geology at the University of California. He reports that the mineral assemblage in it indicates that it was derived largely from a basic volcanic source, either andesitic or basaltic. The grains were too small to permit an accurate choice between these alternatives. Since the sediments apparently grade upward into andesites on the slopes above, the beds are probably a part of the extensive emplacements of andesitic materials that occurred in the Sierra Nevada during the Tertiary.

The lower quartz gravels at Remington Hill extend southwestward 7 miles to the lower end of Chalk Bluffs Ridge. Here they are overlain by rhyolitic tuffs, followed by the andesitic tuff-breccia. At Remington Hill, however, the rhyolite tuffs seem to be absent. Unless the bluish-yellow clay represents it, the rhyolitic phase of deposition either did not occur at Remington Hill or was eroded by the cutting of later Tertiary channels before the Remington Hill sediments were laid down.

In a study of the auriferous gravels, Lindgren (1911, pp. 46–48) determined

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with some accuracy the course and former grade of the early Tertiary quartz-gravel channels in this area. The channel of which Remington Hill is a part apparently came down what is now a small ridge between the forks of Steep Hollow Creek 2 to 3 miles east of Remington Hill. Here it turned west to Democrat, ¾ mile east, thence to Remington Hill and southeast across Steep Hollow Creek and Bear River. At Little York on the ridge between Steep Hollow Creek and Bear River, about 7 miles southwest of Remington Hill, the channel turned northwest 3 to 4 miles through You Bet and Red Dog at the lower end of Chalk Bluffs Ridge. It then extended northward to North Columbia, 9 miles distant, where it joined the main channel, which extended west-southwest to Smartsville; beyond this it is no longer traceable.

The method Lindgren used to determine the former grade of the channels is as follows: Since it appears from field evidence that the Sierra Nevada was uplifted in the Tertiary as a block hinged on the southwest side and faulted on the northeast side, the channels of pre-uplift date would be affected in various ways. Those which lie in a southwest direction would become steepened; those in a northeast direction would become flattened, or even reversed; and those in a northwest or southeast direction would be unaffected. The profiles of the present grades of some of the important Tertiary channels are set forth on plate 10 in Lindgren's paper. On this, the following grades of the main fork of the Tertiary Yuba River, which is connected with Remington Hill, are noted:

Blue Tent to Hunt's Hill	NNW	8 miles	33 feet per mile
Hunt's Hill to Little York	NNW	5 miles	17 feet per mile
Iowa Hill to Big Dipper	NNW	3 miles	10 feet per mile

Since the lowest grade shown in this table occurs highest in the channel, the variation cannot be due to the normal concave stream profile. Evidently the changing grade is more directly affected by the former local topography. This variation would be exaggerated perhaps by the relatively short stretches measured. The mean of these figures, giving due weight to the distances they cover, amounts to a little under 24 feet per mile. The length of the channel as traced from Smartsville to Remington Hill is about 70 miles. Multiplying these figures gives 1680 feet as the former elevation of Remington Hill.

This figure is subject to several corrections of undetermined value. The former elevation of the lower end of the channel at Smartsville is not known, although it was probably close to sea level. Small faults occur in the region, which, although the throw along them is small, would affect the final result. The relative shortness of the measured stretches allows opportunity for error to enter the calculation. The later channel system has not been traced with sufficient detail to permit measurement of former grades. If, as Lindgren believes (1911, p. 45), an uplift of the region occurred between the filling of the two sets of channels, there is probably a discrepancy of several hundred feet between the true and the calculated elevation. Owing chiefly to this fact, the calculated elevation must be taken as a minimum. It may be justifiable to assume, therefore, that the elevation of the Remington Hill leaf-bearing beds at the time of deposition was not less than 1700 feet, and probably about 2000 feet.

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As Lindgren has stated, the erosion of the later channel system resulted in narrow valleys and canyons, often cut to a depth of 200 or 300 feet, in both the bedrock and the older set of filled channels. The topography of the region may thus be pictured as a system of fairly deep and narrow canyons winding generally southwestward, occasionally flanked by depositional terraces and interspersed with rounded knobs and ridges underlain by bedrock. Streams flowed slowly in the canyons, depositing fine-grained material with occasional gravel bars. Most of the finer sediments were of volcanic materials derived from eruptions in higher parts of the range to the east, which represented the opening stages of the extensive outpourings that a little later would almost completely bury the region around Remington Hill. Differences in elevation between the canyon floors and the tops of the ridges may have amounted to as much as 1000 feet.

Composition and Physical Indications

The Remington Hill flora consists of 33 species, of which 1 is of uncertain position. The remaining species are distributed among 24 genera in 19 families and 12 orders. Two of these are gymnosperms, one a monocotyledon, and the others dicotyledons. Nearly 1500 specimens represent the flora from both localities, including those examined in the field and those brought to the laboratory for study.

Systematic List of Species

Spermatophyta
- Gymnospermae
  - Coniferales
    - Taxodiaceae
      - Sequoia langsdorfii (Brongniart) Heer
    - Cupressaceae
      - Chamaecyparis gracilis new species
- Angiospermae
  - Monocotyledones
    - Liliales
      - Liliaceae
        - Smilax diforma Condit
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Populus alexanderi Dorf
        - Populus pliotremuloides Axelrod
        - Populus prefremontii Dorf
        - Salix hesperia (Knowlton) new combination
    - Juglandales
      - Juglandaceae
        - Juglans pseudomorpha new species
    - Fagales
      - Fagaceae
        - Quercus douglasoides Axelrod

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Quercus prelobata new species
Quercus pseudo-lyrata Lesquereux
Quercus remingtoni new species
Quercus simulata Knowlton
Quercus winstanleyi Chaney
Quercus wislizenoides Axelrod

Urticales
Ulmaceae
Ulmus californica Lesquereux

Ranales
Berberidaceae
Mahonia malheurensis Arnold
Lauraceae
Persea pseudo-carolinensis Lesquereux
Umbellularia salicifolia (Lesquereux) Axelrod

Rosales
Hamamelidaceae
Liquidambar pachyphyllum Knowlton
Platanaceae
Platanus paucidentata Dorf
Rosaceae
Crataegus newberryi Cockerell
Prunus petrosperma new species

Sapindales
Aceraceae
Acer negundoides MacGinitie
Hippocastanaceae
Aesculus preglabra new species
Sapindaceae
Ungnadia clarki new species

Rhamnales
Rhamnaceae
Berchemia multinervis (Al. Braun) Heer
Ceanothus precuneatus Axelrod
Vitaceae
Vitis bonseri Berry

Ericales
Ericaceae
Arbutus matthesii Chaney
Arctostaphylos martzi new species

Rubiales
Caprifoliaceae
Viburnum platyspermum new species

Incertae sedis
Abies ? sp.

The Fagales is the most abundant order, being represented by 7 species, all oaks. The Rosales and Salicales are represented by 4 species, the Sapindales, Ranales, and Rhamnales by 3 species, the Ericales and Coniferales by 2, and the remaining orders by 1 species each. Of the 32 identifiable species, 9 are new in

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this flora. Table 2 gives the relative abundance of the Remington Hill species. Stream-border trees such as sycamore (*Platanus paucidentata*) and willow (*Salix hesperia*) are most abundantly represented. The oaks and elm (*Ulmus californica*) also have durable leaves and are among the more common species at Remington Hill, although rare or absent at Oakvale Mine. Seven species make up 90 per cent of the collection, and 5 more account for another 6 per cent, leaving 4 per cent for the remaining 21. These proportions may not represent accurately the relative abundance of the species, since the specimens come from only two localities, but they indicate the common plants near the sites of deposition.

TABLE 2

NUMBER OF SPECIMENS REPRESENTING EACH SPECIES IN THE REMINGTON HILL FLORA

Species	*Remington Hill*	*Oakvale Mine*	*Total specimens*	*Per cent*
Quercus remingtoni	321	9	330	22
Platanus paucidentata	274	12	286	19
Salix hesperia	194	41	235	16
Quercus prelobata	203	2	205	14
Quercus douglasoides	105	3	108	7
Ulmus californica	105	0	105	7
Quercus pseudo-lyrata	43	32*	75	5
Liquidambar pachyphyllum	20	0	20	2
Crataegus newberryi	15	0	15	1
Ungnadia clarki	0	12	12	1
Acer negundoides	11	0	11	1
Umbellularia salicifolia	8	3	11	1
Mahonia malheurensis	8	0	8	
Quercus simulata	8	0	8	
Populus prefremontii	5	2	7	
Sequoia langsdorfii	6	0	6	3
Aesculus preglabra	5	0	5	
Quercus wislizenoides	5	0	5	
Berchemia multinervis	1	4	5	
Populus alexanderi	4	1	5	
Prunus petrosperma	3	0	3	
Abies ? sp.	1	0	1	
Arbutus matthesii	1	0	1	
Arctostaphylos martzi	1	0	1	
Ceanothus precuneatus	1	0	1	
Chamaecyparis gracilis	1	0	1	
Juglans pseudomorpha	1	0	1	1
Persea pseudo-carolinensis	1	0	1	
Populus pliotremuloides	1	0	1	
Quercus winstanleyi	1	0	1	
Viburnum platyspermum	1	0	1	
Vitis bonseri	1	0	1	
Smilax diforma	0	1	1	
Total	1355	122	1477	100

*Includes count made by R. W. Chaney at Oakvale Mine in 1930.

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On the basis of the geographic occurrence of living equivalent species, it is possible to recognize four elements in the flora. They are largely distinct, although a few species occur in more than one. In some cases, for example

TABLE 3

ELEMENTS AND COMPONENTS OF THE REMINGTON HILL FLORA

Fossil species	*Equivalent living species*
West American Element	
Redwood Component	
Chamaecyparis gracilis	C. lawsoniana Parlatore
Sequoia langsdorfii	S. sempervirens Endlicher
Umbellularia salicifolia	U. californica Nuttall
Border-redwood Component	
*Acer negundoides	A. negundo var. californicum Sargent
Arbutus matthesii	A. menziesii Pursh
*Juglans pseudomorpha	J. californica Watson
Platanus paucidentata	P. racemosa Nuttall
Populus alexanderi	P. trichocarpa Torrey and Gray
Populus pliotremuloides	P. tremuloides Michaux
Quercus prelobata	Q. lobata Née
Quercus pseudo-lyrata	Q. kelloggii Newberry
Quercus remingtoni	Q. morehus Kellogg
Salix hesperia	S. lasiandra Bentham
Viburnum platyspermum	V. ellipticum Hooker
Southwest American Element	
Oak woodland Component	
Populus prefremontii	P. fremontii Watson
*Prunus petrosperma	P. ilicifolia Walpers
Quercus douglasoides	Q. douglasii Hooker and Arnott
Quercus wislizenoides	Q. wislizenii A. DeCandolle
Ungnadia clarki	U. speciosa Endlicher
Chaparral Component	
Arctostaphylos martzi	A. manzanita Parry
Ceanothus precuneatus	C. cuneatus Nuttall
Mahonia malheurensis	M. haematocarpa (Wooton) Fedde
*Prunus petrosperma	P. ilicifolia Walpers
East American Element	
*Acer negundoides	A. negundo Linnaeus
Aesculus preglabra	A. glabra Willdenow
Berchemia multinervis	B. scandens Trelease
*Juglans pseudomorpha	J. nigra Linnaeus
Liquidambar pachyphyllum	L. styraciflua Linnaeus
Persea pseudo-carolinensis	P. borbonia Sprengel
*Quercus winstanleyi	Q. prinus Linnaeus
Smilax diforma	S. rotundifolia Linnaeus
Ulmus californica	U. americana Linnaeus
East Asian Element	
Crataegus newberryi	C. pinnatifida Bunge
Quercus simulata	Q. myrsinaefolia Blume
*Quercus winstanleyi	Q. aliena Blume

*Species occurring in more than one component.

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Juglans pseudomorpha, modern species considered equally related to the fossil are found in different areas. Out of 31 species which give evidence of modern relationships, 14 represent the Redwood and Border-redwood Components of the West American Element and 8 represent the Oak woodland and Chaparral Components of the Southwest American Element; together these make up 89 per cent of the collections.

The Redwood Component finds its living equivalent species ranging along the coast from southwestern Oregon into central California. Throughout this region they border diverse types of vegetation, ranging from humid coniferous forests at the north to woodland and chaparral at the south and interior. In view of the association of the Border-redwood, Oak woodland, and Chaparral Components with the Redwood at Remington Hill, attention is directed to the Santa Lucia Mountains of coast-central California, an area where the living equivalents of 16 of the 22 species representing these four components grow close together.

The Santa Lucia range trends in a southeasterly direction, rising steeply from the sea. On the north, adjacent to the valley of the Carmel River, vegetation may be found which closely resembles the greater part of that preserved at Remington Hill. In the valleys and canyons on the seaward and northward slopes of the range is a forest of *Sequoia sempervirens* and *Umbellularia californica,* with their regular associates of tan oak, big-leaf maple, and alder. Only *Chamaecyparis* of the Redwood Component is not represented here; it ranges inland, however, at the north, where it approaches a border-redwood forest closely similar to that represented in the Remington Hill flora. The rarity of both the redwood and the cedar at Remington Hill suggests that they lived in canyons at some distance from the sites of deposition. The restriction of redwood to deep canyons in the Santa Lucia Mountains 1 or 2 miles from the Carmel River flood plain, in a region dominated by members of a border-redwood forest, is highly suggestive of Remington Hill conditions. Modern equivalents of the Border-redwood Component in the northern Santa Lucia Mountains include most of the species listed in table 3. *Platanus racemosa, Populus trichocarpa,* and *Salix lasiandra* are common along the Carmel River, and *Acer negundo* var. *californicum* is a frequent associate. *Arbutus menziesii, Quercus lobata, Q. kelloggii,* and *Q. morehus* are among the conspicuous forest trees on slopes adjacent to the redwood forest and occur with it in the canyons. The equivalent species of the Border-redwood Component in this region significantly include all the Remington Hill dominants. Only two equivalents of the Border-redwood Component are not represented here. *Viburnum ellipticum* ranges from Washington to Sonoma County, north of San Francisco Bay, where it is found with many modern equivalents of the Remington Hill flora representing the Redwood and Border-redwood Components. The walnut, *Juglans pseudomorpha,* has a related species in *J. californica* of southern California, as well as in *J. hindsii* of the inner north Coast Range bordering Sacramento Valley. This latter species is found along streams with numerous representatives

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of the Border-redwood and Oak woodland Components that range into the Santa Lucia region.

Living vegetation representing the Oak woodland and Chaparral Components of the Remington Hill flora is common in the northern Santa Lucia Mountains. The cottonwood, *Populus fremontii,* occurs along the Carmel River with *Platanus racemosa, Populus trichocarpa, Acer negundo* var. *californicum,* and *Salix lasiandra. Quercus douglasii,* which attains optimum development under the drier climate of the interior, reaches coastward on exposed slopes and is found with redwood and its associates at no great distance from the coast. Chaparral in this region, including the species of *Arctostaphylos, Ceanothus,* and *Prunus* represented by equivalents in the Remington Hill flora, is found largely on dry, steep slopes. Its species frequently mingle with the oak woodland and border-redwood communities. Only two members of the Oak woodland Component are not represented in this region by equivalent species. *Ungnadia speciosa* and *Mahonia haematocarpa* are now limited to parts of the southwestern United States and northern Mexico where there are regular summer showers.

Climatic data for the lower flanks of the Santa Lucia Mountains and the adjacent Carmel River valley may be estimated from a 23-year record at Del Monte, which lies 10 miles northwest at an elevation of 40 feet. Conditions are as shown in table 4. Rainfall on the lower slopes of the Santa Lucia Mountains

TABLE 4

CLIMATIC DATA FOR DEL MONTE, CALIFORNIA

Month	Monthly and annual av. temperature (°F.)	Monthly and annual av. precipitation (in.)
January	49.6	3.58
February	51.8	2.75
March	54.2	2.55
April	56.2	0.74
May	57.7	0.42
June	60.0	0.10
July	61.4	Trace
August	61.6	0.10
September	62.0	0.31
October	58.6	0.46
November	53.7	1.42
December	50.1	2.89
Annual	56.4	15.33 (total)

in the Carmel Valley is undoubtedly higher than at Del Monte, because of greater elevation. Judging from the 40-inch yearly rainfall at Big Sur 20 miles southward, an average yearly rainfall of 35 inches may be estimated for the northern end of the Santa Lucia Mountains adjacent to the Carmel River valley 4 to

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5 miles from the coast, where most of the species named above now live. Winter temperatures here are probably slightly lower than at Del Monte, where the moderating effects of the ocean are greater, and summers are warmer in the Carmel River valley than at Del Monte. Summer fogs commonly extend up the valley, but they disappear by midmorning, whereas in the immediate coastal area they may persist for a number of days.

Nine Remington Hill species, making up 10 per cent of our specimens, form the East American Element. Three of these occur in other elements: *Acer negundoides* and *Juglans pseudomorpha* in the West American, and *Quercus winstanleyi* in the East Asian. The East American Element is a regular part of the Arcto-Tertiary Flora and is associated typically with members of the Redwood and Border-redwood Components in the Miocene of the western United States. Modern descendants of this group make up a prominent part of the forests in the eastern United States at latitudes ranging from 28° to 48°, but centering between 30° and 37°. This distribution falls a few degrees south of the latitude of the distribution of equivalent species of the Redwood and Border-redwood Components now in California.

A major difference between the climates of the eastern United States and central California is that the latter has a marked dry season in the summer months, with rainfall concentrated during winter and early spring; in the eastern United States rainfall is more evenly distributed over the year. It may be suggested that since the Redwood, Border-redwood, and Oak woodland Components are much better represented than the East American Element in our collections, seasonally distributed rainfall with dry summers is indicated. Paleobotanical evidence suggests, however, that living equivalent species of these components may have become adapted to a dry season in comparatively late geologic time. Out of 22 species which appear most closely related to plants now living in summer-dry regions on the Pacific coast, 10 have close relatives in older and more northern fossil floras in company with a large number of plants suggesting a rainfall regime similar to that of eastern North America. The evidence of the contemporaneous Neroly flora suggests that summer rain was present in the region at the time of deposition.

The few species related to plants now found in southwestern North America also support the assumption of summer rain, since the modern equivalents are found in regions where rainfall occurs commonly in both summer and winter. In the northern part of its range, *Ungnadia speciosa* is a typically desert stream-border tree, but to the south it is also found on open slopes of the mountains of eastern Mexico under conditions of moderate temperature and abundant, evenly distributed rainfall (H. D. MacGinitie, written communication, November 1939). *Mahonia haematocarpa,* regarded as the equivalent of *Mahonia malheurensis,* is common with woodland and chaparral vegetation in the southwestern United States and may grow there with *Ungnadia speciosa.*

Little precise information concerning the climatic requirements of the East Asian species is available. *Quercus myrsinaefolia* lives at temperate elevations in western and southern China. The remainder are common at moderate

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altitudes in northern and central China, where conditions are similar to those suggested by the East American Element. It is significant also that these fossils related to living Asiatic species occur with the Arcto-Tertiary Flora in company with species indicating temperate, humid climate.

The evidence thus strongly favors the conclusion that in the Sierra Nevada at the time of deposition of the Remington Hill flora, the climate was marked by moderate extremes of temperature, with freezing rare in winter and summers not excessively hot, and with 35 to 40 inches of annual rainfall having winter and summer maxima. The conditions postulated suggest marked changes in the Remington Hill region since Mio-Pliocene time.

The present climate of the area may be termed moist temperate. No weather records are available for the fossil locality, but data from two adjacent stations serve to indicate climatic conditions more precisely, as set forth in table 5. Inas-

TABLE 5

CLIMATIC DATA FOR STATIONS ADJACENT TO REMINGTON HILL, CALIFORNIA
(ELEVATION 3840 FEET)

MONTH	MONTHLY AND ANNUAL AV. TEMPERATURE (°F.)		MONTHLY AND ANNUAL AV. PRECIPITATION (in.)	
	Blue Canyon*	Deer Creek†	Blue Canyon	Deer Creek
January	36.8	35.8	13.63	16.36
February	38.2	38.7	11.45	12.41
March	40.2	41.6	10.39	9.81
April	46.0	47.2	4.17	4.23
May	50.5	52.0	3.29	3.26
June	58.0	58.8	0.93	0.94
July	64.2	65.6	0.08	0.06
August	64.0	65.1	0.09	0.06
September	59.5	59.4	1.21	1.26
October	54.1	51.8	3.54	2.98
November	45.6	43.3	6.85	6.42
December	40.0	36.7	9.64	11.75
Annual	49.8	49.7	65.27‡	69.54‡

*Four miles east of Remington Hill, elevation 4695 feet.
†Six miles west of Remington Hill, elevation 3700 feet.
‡Total.

much as Remington Hill lies between Blue Canyon and Deer Creek, both geographically and altitudinally, it may be assumed that averages for these two stations would approximate the precipitation and temperature now prevailing at the fossil locality. If records were available for Remington Hill, it would probably be found to have a mean annual temperature slightly less than 50° F., with average winter temperatures about 38° and average summer temperatures approximately 62.6° F. Mean annual precipitation may be estimated

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at 67 inches, with almost three-quarters of it falling in the four winter months, and only a little more than an inch distributed among the three summer months. Much of the winter precipitation is in the form of snow, which remains on the ground in protected places well into the spring months, thus making more water available for plants during the growing season than is indicated by the figures.

It may be concluded that the mean annual temperature of Remington Hill time was somewhat higher, with winter temperatures higher than today; summer temperatures were lower than the present summer mean of about 62.6° F. Rainfall was approximately 35 to 40 inches annually, or about 30 inches less than at present, with no prolonged summer drought. The difference in amount of yearly rainfall may be ascribed to increased elevation since Remington Hill time, but the difference in distribution through the year must be attributed to more fundamental climatic changes. These differences suggest that the climate of the region was more immediately affected by the ocean than is now the case, and are also in accord with evidence that the climate of later Tertiary time in western North America was somewhat warmer than at present. The Coast Ranges to the west were lower and less continuous, and consequently did not form such an effective barrier to moisture-bearing winds from the Pacific as they do today.

The evidence regarding physical conditions during the Remington Hill stage may be summarized as follows:

1. The fluviatile sediments containing the flora were deposited in deep, relatively narrow canyons situated in rolling country approximately 2000 feet above sea level on the middle slopes of the central Sierra Nevada.

2. Dominant in the flora are members of the Border-redwood Component of the West American Element. Redwood Component species lived in protected canyons above the sites of deposition, and here also were representatives of the East Asian and East American Elements in small numbers. Adjacent exposed slopes were occupied by representatives of the Oak woodland and Chaparral Components of the Southwest American Element.

3. Remington Hill climate was characterized by 35 to 40 inches of annual rainfall, with important amounts in the summer as well as in the winter months. Winter and summer temperatures were more moderate than those of today, showing a greater oceanic influence.

Age of the Flora

In a previous section it was pointed out that the beds containing the fossil leaves were probably derived from an andesitic source, and hence are part of the great andesitic extrusions of the Sierra Nevada. For many years the andesitic phase of deposition on the western flanks of the Sierra Nevada has been regarded as late Tertiary, although little direct evidence for such a supposition was forthcoming from the mountains themselves. Inasmuch as the streams of the ancestral Sierra Nevada drained westward into an inland sea occupying the area which is now the Great Valley and Coast Ranges of California, it is evident that large additions to the material carried by those streams should appear in

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the prism of sediments laid down in that sea, unless they were all removed by erosion during a subsequent stage of emergence. There are now known to be at least two sets of beds in the Great Valley which are predominantly of andesitic debris, and it is reasonable to assume that the Remington Hill beds may be contemporaneous with one or the other of them. The earlier of these, the Wheatland formation, has been discussed by Clark and Anderson (1938). This formation is exposed 6 miles northeast of Wheatland, Yuba County, and lies about 25 miles southwest of Remington Hill, near the mouth of the Tertiary Yuba River. It is composed of marine and swamp deposits ranging from conglomerates to fine shales. Enclosed invertebrate remains indicate that the beds were deposited during the Upper Eocene or the Lower Oligocene. The material appears to have been derived from the Sierra Nevada, and consequently must be considered as a possible correlative of the beds at Remington Hill. Paleobotanical evidence is strongly opposed to such a suggestion. All the Lower Tertiary floras found in middle latitudes of western North America have a large proportion of genera now restricted to subtropical regions of the world. The LaPorte flora (Potbury, 1935), from a locality 30 miles north of Remington Hill at a similar elevation, and assigned to approximately the same age as the Wheatland formation, contains 34 genera, of which only 6 are also present in the Remington Hill community; a single species (*Persea pseudo-carolinensis*) is common to the two. Such genera as *Davilla, Hyperbaena, Petrea, Cinnamomum, Columbia,* and *Microdesmis,* which are now found only at low latitudes, are indicative of an age older than Remington Hill. This assemblage has been interpreted as indicating a climate characterized by a mean annual temperature of about 75° F., and a yearly rainfall of 65 inches. In view of the relatively short distance separating this flora from Remington Hill, the wide discrepancies in specific content and indicated climate must be ascribed to a difference in age. Thus the Remington Hill sediments cannot be considered contemporaneous with the Wheatland formation.

A later, as well as a more widespread, occurrence of andesitic material in the Great Valley and Coast Ranges is in the Neroly and Sutter formations. The Neroly crops out in the middle Coast Ranges and has been observed also in well cores from the western side of the Great Valley. Vertebrate, invertebrate, and paleobotanical evidence has all been interpreted as indicating a late Miocene or early Pliocene age for the Neroly. Differences of opinion exist as to its position relative to the standard European scale, but there is substantial agreement as to its position in the California column. The Sutter formation is exposed on the sides of the Marysville Buttes, about 50 miles west of Remington Hill and 25 miles west of Smartsville, near the supposed mouth of the Tertiary Yuba River. As described by Dickerson (1916, pp. 403–406), and discussed more fully by Williams (1929), it is composed of tuffaceous sediments of which the upper part is andesitic. Williams considered this to be equivalent to the andesitic tuff-breccias of the Sierra Nevada and the Neroly formation. He writes, in part: "When . . . the detailed petrographic characters of the latter rocks [the Tertiary volcanics of the Sierra Nevada] are compared with those of the Sutter

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tuff, the similarities are seen to be so close that the probability of a common origin amounts almost to certainty." Additional evidence for an eastern source for the Sutter formation is found in the increased thickness and coarseness of the eastern exposures as compared with the western. Williams' discussion shows that he had little doubt that the Sutter was derived from a source to the east, and that the upper andesitic part was contemporaneous with the andesitic tuff-breccias of the western slope of the Sierra Nevada. In the absence of any paleontological evidence from the Sutter formation, the possibility of its being of the same age as the Wheatland must be admitted.

The Sutter formation is of importance in this study only in that it serves as a geographically intermediate exposure between the Neroly formation and the Sierran andesitic tuff-breccias. The evidence for correlating these beds was discussed by Williams, and more fully by Louderback (1924). Both lithologic and distributional evidence strongly supports such a correlation. Andesitic material in well cores has been identified as part of the Neroly formation from under the floor of the Great Valley, where it is considerably thicker than in surface exposures in the Coast Ranges (A. Huey, oral communication, April 1937). These facts suggest that the andesitic tuff-breccias at Remington Hill are of Upper Miocene or Lower Pliocene age. The only published mention of the age of the Remington Hill flora was by Chaney (1932, p. 300), who correlated the Oakvale Mine florule with the Upper Miocene Mascall of Oregon. The Remington Hill flora has now been more completely studied, and the following discussion will set forth its age relations more fully.

Table 6 lists the occurrences of Remington Hill species in other fossil floras in the western United States. Twenty-four of its 32 identifiable species appear in this table. The Weaverville, Bridge Creek, and Eagle Creek floras, ranging from Lower Oligocene to Lower Miocene in age, include 10 of them and 3 others that are closely related. Eight of the identical species, *Acer negundoides, Arbutus matthesii, Berchemia multinervis, Liquidambar pachyphyllum, Persea pseudo-carolinensis, Quercus simulata, Salix hesperia,* and *Sequoia langsdorfii,* range up into the Pliocene, with only *Crataegus newberryi* and *Quercus pseudo-lyrata* limited to floras of pre-Pliocene age. Three additional species in these older floras, *Populus eotremuloides* Knowlton, *Quercus columbiana* Chaney, and *Ulmus speciosa* Newberry, differ from *P. alexanderi, Q. winstanleyi,* and *U. californica* in having leaves of greater dimensions. They are considered ancestral to the Remington Hill species, which show reduction in leaf size in response to increased aridity later in the Tertiary.

The Middle and Upper Miocene floras of the Columbia Plateau and northern Great Basin contain 11 identical Remington Hill species and 5 related species. Three of the species, *Chamaecyparis gracilis, Mahonia malheurensis,* and *Vitis bonseri,* have not been recorded in the Lower Miocene and older floras of this region. Eight species range into the Pliocene, including the cedar. A similar *Vitis* is represented in the Pliocene Dalles flora by a leaf impression (chap. 11 below). Only *Mahonia malheurensis* and *Quercus pseudo-lyrata* are

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TABLE 6

DISTRIBUTION OF REMINGTON HILL SPECIES IN OTHER FOSSIL FLORAS

SPECIES (Total, 24)	OLIGOCENE AND LOWER MIOCENE			MIDDLE AND UPPER MIOCENE				TRANSITIONAL			PLIOCENE			
	Weaverville	Bridge Creek	Eagle Creek	Latah	Payette	Mascall	Trout Creek	Table Mountain	Neroly	Lower Idaho	Mount Eden	Mulholland	Other California Pliocene	Oregon Pliocene
Acer negundoides	...	x	x	x	...	x	x	...	...	x	...	...	....	x
Arbutus matthesii	...	x	...	x	...	x	...	x	...	...	...	x	x	....
Berchemia multinervis	x	...	...	...	...	...	...	x	x	...	...	x	....	....
Ceanothus precuneatus	...	...	...	...	...	...	...	...	...	...	x	...	x	x
Chamaecyparis gracilis	...	...	...	...	...	x	x	...	...	...	...	...	....	x
Crataegus newberryi	...	x	...	...	...	o	...	x	...	...	...	...	....	....
Liquidambar pachyphyllum	...	o	x	x	...	x	...	...	...	...	...	...	....	x
Mahonia malheurensis	...	...	...	...	...	...	x	...	...	...	...	...	....	....
Persea pseudo-carolinensis	x	...	...	...	...	...	...	...	x	...	...	...	x	....
Platanus paucidentata	...	...	...	...	...	...	...	...	...	...	x	x	x	....
Populus alexanderi	...	...	o	...	o	...	...	...	o	o	...	x	x	x
Populus pliotremuloides	...	...	...	...	o	o	o	...	...	...	x	...	x	x
Populus prefremontii	...	...	...	...	...	...	...	...	...	...	...	x	x	....
Quercus douglasoides	...	...	...	...	...	...	...	...	...	...	x	...	x	....
Quercus pseudo-lyrata	...	...	x	...	...	x	...	...	...	...	...	...	....	....
Quercus simulata	...	o	x	x	x	x	x	...	...	x	...	x	....	....
Quercus winstanleyi	...	...	o	o	...	o	...	...	...	o	...	...	....	x
Quercus wislizenoides	...	...	...	...	...	...	...	...	...	...	...	x	x	....
Salix hesperia	x	...	...	x	x	x	...	...	x	x	...	x	x	x
Sequoia langsdorfii	...	x	...	x	x	x	...	...	...	x	...	...	x	x
Smilax diforma	...	...	...	...	...	...	...	...	x	...	...	...	....	....
Ulmus californica	...	o	o	o	...	o	...	x	...	o	...	...	x	x
Umbellularia salicifolia	...	...	...	x	...	x	...	x	x	...	...	x	x	x
Vitis bonseri	...	...	...	x	...	...	...	...	...	...	...	...	....	o
Identical species	3	4	4	8	3	9	4	5	5	4	4	9	13	11
Related species	0	3	3	2	2	4	1	0	1	3	0	0	0	1
Identical species in epoch		10			11				11			19		
Related species in epoch		3			5				2			1		

x = identical species; o = related species.

not known from post-Miocene floras. Three of the 5 related species in these floras are the wide-ranging cottonwood, oak, and elm discussed above. The fourth is *Populus lindgreni* Knowlton, which also has larger leaves than *P. pliotremuloides;* the fifth is the Mascall *Crataegus imparilis* Knowlton, which may not be distinct from *C. newberryi.* These relationships likewise suggest that if the flora is Miocene it belongs to the latest part of that epoch.

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The Table Mountain, Neroly, and Lower Idaho floras are listed in this table as transitional Mio-Pliocene. They include a total of 11 Remington Hill species, in addition to the related oak and cottonwood. In this connection, it is significant that the Table Mountain and Lower Idaho floras contain the smaller-leafed *americana* type of elm, *U. californica,* rather than the larger *U. speciosa,* which is typical of the Miocene. These transitional Mio-Pliocene floras contain only 1 species, *Smilax diforma,* that is restricted to this stage. All the others are known from both Miocene and Pliocene floras, except *Crataegus newberryi,* which is limited to older horizons.

Nineteen Remington Hill species are represented in Pliocene floras of the western United States; 11 of these are in the Oregon Pliocene and 15 in the Pliocene of California. Such species as *Ceanothus precuneatus, Platanus paucidentata,* and *Populus prefremontii* are also recorded in the Miocene of southern California, but are not known at the latitude of Remington Hill until late in the Miocene or early Pliocene; *Quercus douglasoides* and *Q. wislizenoides* also belong to this group, though they have not yet been recorded in pre-Pliocene floras. The remainder occur in the Miocene to the north or are represented there by presumably ancestral species. Such species as *Ulmus californica, Populus pliotremuloides, P. alexanderi,* and *Quercus winstanleyi* clearly give a Pliocene aspect to the Remington Hill flora.

In summary, table 6 indicates 14 Remington Hill species, and 4 others showing close relationship, in floras of Oligocene and Miocene age, with only 2 limited to these epochs. Eleven species, as well as 2 related ones, are in transitional Mio-Pliocene floras, and 1 is restricted to this stage. Nineteen are in the Pliocene, with 5 confined to this epoch. These relationships suggest a transitional Mio-Pliocene age for the flora.

An inspection of the numerical occurrence of species in other fossil floras does not always provide an adequate basis for age determination. The composition of the flora in question must be considered in the light of what is known concerning the Tertiary migrations of forests, and the resulting changes in their composition that have taken place in one area at different times since the Cretaceous. This is particularly important in the case of a flora deposited at some distance from the sea in either a horizontal or a vertical direction, since profound changes in floral composition may be produced by the alteration of climate due to topographic changes. This concept has been enunciated and illustrated in several papers in recent years (Chaney, 1936*a*, 1938*b*, 1940). Accordingly, the Remington Hill flora may be further examined from the standpoint of its relations to other Tertiary floras of western North America.

The relationship of the Remington Hill to the Upper Miocene floras of Oregon, Washington, and Idaho might be considered as suggesting an Upper Miocene age for this flora. But whereas most of the northern floras lived within 1000 feet of sea level, the Remington Hill flora appears to have existed at approximately 2000 feet. Modern vegetation in western North America increases the altitude of its range by about 400 feet for every degree of latitude, and there

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is no reason to assume that this relation was different in the past. Since 5 or 6 degrees of latitude separate the Remington Hill from the similar Mascall and related floras to the north, we might expect a difference of from 2000 to 2400 feet; hence, a difference in elevation of only 1000 feet would indicate that these two floras were not contemporaneous. In other words, a typically Upper Miocene flora in the central Sierra Nevada would be expected at elevations above that of the Remington Hill flora. The similarity between these floras also suggests a difference in age, since a time interval would be required during which the species of the Upper Miocene forests in the north could migrate southward to become members of the forest at Remington Hill. These facts suggest that the Remington Hill flora is younger than the Mascall and related floras at the north, even though they have many species in common. In other words, its age is approximately the same as that of the Neroly. The presence of only 5 species common to the Remington Hill and Neroly may be explained on the basis of differences in elevation and habitat. Whereas the Neroly forest lived at sea level, probably in swamps at the mouths of streams, the Remington Hill grew about 2000 feet higher. These differences assume critical importance at the close of the Miocene, when all of western North America was being subjected to important climatic changes.

Of the 15 Remington Hill species recorded in the California Pliocene, only 7, *Ceanothus precuneatus, Platanus paucidentata, Populus alexanderi, P. pliotremuloides, P. prefremontii, Quercus douglasoides,* and *Q. wislizenoides,* may be regarded as characteristic of that epoch at this latitude. The relatively poor representation of all except the sycamore is interpreted to indicate that the age of the flora is not younger than early Pliocene. Another consideration confirms this age determination. Axelrod has pointed out that the uppermost Miocene and Lower Pliocene in central California are marked by an invasion of the Madro-Tertiary Flora, a group of semiarid woodland and chaparral plants, from the south and southeast, with subsequent southward restriction of some of them in the late Pliocene. There appear to be 8 species in the Remington Hill flora that may be considered to belong to the Southwest American Element. Inasmuch as they make up only a small part of the flora, it would appear that it lived either before or after the maximum invasion of the element. A late Pliocene age is not likely, in view of the close relationship to Miocene floras. The Table Mountain flora, which is essentially transitional Mio-Pliocene in age, includes a large representation of the Southwest American Element. Since the Remington Hill is considered to be of the same age, it must have lived near the upper altitudinal limits of this semiarid vegetation, in much the same manner that the Remington Hill area lies in a moister zone above the digger pine woodland today. This age reference is supported by the presence of such typical Miocene derivatives as *Populus pliotremuloides, P. alexanderi,* and *Ulmus californica* in the flora. They likewise suggest that the trend to aridity in western North America had progressed sufficiently by Remington Hill time to permit the Southwest American Element to occupy the middle slopes of the

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range. It is therefore believed that the Remington Hill flora was laid down near the upper altitudinal limits of this southern flora which invaded the western flanks of the central Sierra Nevada in transitional Mio-Pliocene time.

A few years ago a small collection of fossil leaves was made by H. D. MacGinitie from the dump of an abandoned drift mine near Forest, Sierra County, California, 12 miles north of Remington Hill and at essentially the same elevation. Since it is unlikely that further collections will be made from this locality, and because the florule bears considerable resemblance to the Remington Hill flora, it will be discussed briefly at this time. The leaves occur in a gray, sandy clay similar to the material at Remington Hill. MacGinitie reports that this clay is associated with gravels lying directly below extensive andesitic deposits. This stratigraphic position is the same as that of the Remington Hill flora, and suggests an identical age. The following species have been noted in the collection:

Aesculus preglabra
Ceanothus precuneatus (?)
Platanus paucidentata
Salix hesperia
Smilax diforma
Ulmus californica
Ungnadia clarki
Fraxinus sp. (seed)
Legumes (2 species)
Magnolia (?)
Nyssa (?)
Pinus sp.
Quercus sp.

This list shows extremely close correspondence with the composition of the Remington Hill flora, and amply supports the stratigraphic evidence that the Forest florule is contemporaneous with the Remington Hill flora. The florule establishes the fact that the community represented at Remington Hill was widespread over the ancestral Sierra Nevada, as is the modern vegetation in the same area.

Summary

The Remington Hill flora, comprising 32 identifiable species, occurs in andesitic sediments equivalent to the lower Mehrten formation, deposited in the upper foothills of the central Sierra Nevada. The West American Element is dominant, with members of the East American and East Asian Elements in smaller numbers. The Southwest American Element has a subordinate place here as compared with its representation in the contemporaneous Table Mountain flora, from a lower elevation. The Remington Hill flora lived in a region of diverse relief, under a climate of moderate temperatures and annual rainfall, with more summer precipitation than at present. The subsequent trend to a more continental climate seems related to the elevation of the Coast Ranges at the west, and to important climatic changes in western North America later in the Cenozoic. A transitional Mio-Pliocene age is indicated by geologic and paleobotanical evidence.

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SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class GYMNOSPERMAE
Family TAXODIACEAE

Sequoia langsdorfii (Brongniart) Heer

(Plate 4, figure 1)

Sequoia langsdorfii (Brongniart) Heer, Flora tertiaria Helvetiae, vol. 1, p. 54, pl. 20, fig. 2; pl. 21, fig. 4, 1855.

Several specimens of foliage of this species appear in the collections from Remington Hill. Among the gross characters, the size of the needles, the way in which they are loosely adnate to the twigs, and the thick center-line ridge along the lower surface suggest their identification. In addition, samples of the carbonaceous material found in the impressions were sent to Dr. Rudolf Florin, who reports that the microscopic structure clearly indicates that the fossils are closely related to the living *Sequoia sempervirens* Endlicher (written communication, January 1940).

Sequoia langsdorfii has many times been reported in Tertiary floras of North America, particularly in Oregon, but has only occasionally appeared in deposits of the Sierra Nevada. The living relative of this species is closely restricted to regions where sea fogs are an important part of the climate, and this fact may be brought forward to explain its rarity in deposits more distant from the ocean.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2376, 2376*a* (counterpart); nos. 2377, 2378, 2379, 2380.

Family CUPRESSACEAE

Chamaecyparis gracilis new species

(Plate 4, figure 2)

Libocedrus dimorpha Oliver (in part), Carnegie Inst. Wash. Pub. 455, I, pp. 15–16, pl. 3, fig. 1, 1936.

Description. Leaves decussate, less than 2 mm. long, about 1 mm. wide, triangular, with a prominent gland where surface is well preserved, closely adnate to stem throughout length; stem, when clothed in leaves, less than 2 mm. in diameter.

Discussion. The only previously published occurrence of *Chamaecyparis* from the Tertiary of western North America is in the Upper Cedarville beds of northeastern California and northwestern Nevada (LaMotte, 1936, pp. 112–113, pl. 3, figs. 4, 5). Those specimens were considered to be most closely related to the living *Chamaecyparis nootkatensis* Spach, but in a forthcoming paper on the Molalla flora of Oregon, Wilder shows that they are *Fokienia.* The relationship of *Libocedrus dimorpha* Oliver (1934, pp. 15–16, pl. 3, fig. 1) to the Remington Hill fossil is obscure. Her smallest specimen (paratype no. 657) closely resembles *Chamaecyparis gracilis,* and is probably the same species. The two larger specimens (holotype no. 655 and paratype no. 656) are less similar, differing in the following ways: the leaves appear to be arranged in fours around the stem, rather than in alternate pairs; and long adnate

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leaves are more common than is characteristic of *Chamaecyparis*. It is probable that Oliver assigned two different forms to the same species.

Chamaecyparis lawsoniana Parlatore lives in coastal southern Oregon and northern California, occasionally in company with the redwood, whereas *C. thyoides* Britton, Sterns, and Pogg is found along the coast of the eastern United States from southern Maine to northern Florida, and extends westward to the Mississippi. It is more abundant and better developed in the northern part of its range.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2381.

Class ANGIOSPERMAE
Subclass MONOCOTYLEDONES
Family LILIACEAE

Smilax diforma Condit

(Plate 4, figure 3)

Smilax diforma Condit, Carnegie Inst. Wash. Pub. 476, V, pp. 253–254, pl. 3, figs. 4*b*, 5, 1938.

Only 1 specimen of this species has been noticed in the Oakvale Mine collections. It closely resembles the specimen of *Smilax reticulata* Heer, as figured by Hollick from the Tertiary of Alaska (Hollick, 1936, p. 58, pl. 22, fig. 1), but the great geographic and stratigraphic separation makes it unlikely that the Remington Hill leaf is the same as *S. reticulata*. *Smilax diforma* is somewhat similar to *S. goshenensis* Chaney and Sanborn (1933, pp. 64–65, pl. 4, figs. 1, 3), except that it has a truncate rather than a cuneate base. It differs from *S. magna* Chaney, of the Miocene Eagle Creek formation of Oregon (Chaney, 1920, p. 161, pl. 6, fig. 1), in lacking the pronounced cordate or auriculate base of that species, as well as in its smaller size. It is also considerably smaller than the type specimens of *S. diforma*. Since, however, it is closely matched by leaves of the living *S. rotundifolia* Linnaeus, to which the Neroly specimens were related, it is considered here to be the same species.

Occurrence. Oakvale Mine, loc. 204.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2382.

Subclass DICOTYLEDONES
Family SALICACEAE

Populus alexanderi Dorf

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, figs. 10, 11 (not fig. 9, which is *P. prefremontii* Dorf); pl. 7, figs. 2, 3 (not fig. 1, which is *P. prefremontii*), 1930.

Chaney, Carnegie Inst. Wash. Pub. 476, IV, p. 215, pl. 6, figs. 1, 5; pl. 7, fig. 2, 1938.

Axelrod, Carnegie Inst. Wash. Pub. 516, p. 92, pl. 6, fig. 6, 1939.

Several typical specimens of this characteristic Pliocene poplar occur in the flora. Its nearest descendant, *Populus trichocarpa* Torrey and Gray, has survived down to the present in scarcely modified form in the Remington Hill region.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2383.

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Populus pliotremuloides Axelrod

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 169–170, pl. 4, figs. 1–3, 1938.

A characteristic leaf of the Pliocene aspen comprises the only record of this species in the flora. Its closest living descendant, *Populus tremuloides* Michaux, occurs today in the higher parts of the Sierra Nevada but descends to lower levels and into the Transition forest in areas of favorable topographic relief.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2384.

Populus prefremontii Dorf

(Plate 4, figure 6)

Populus prefremontii Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 77–78, pl. 7, fig. 4, 1930. Axelrod, Carnegie Inst. Wash. Pub. 516, p. 93, 1939.

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, fig. 9 only; pl. 7, fig. 1 only, 1930.

Several well preserved cottonwood leaves are indistinguishable from this Pliocene species. Their modern equivalent, *Populus fremontii* Watson, is common on the lower Sierran slopes and ranges upward into the lower part of the Transition forest.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2386; no. 2385.

Salix hesperia (Knowlton) new combination

(Plate 4, figure 7)

Juglans hesperia Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 723, pl. 99, fig. 8, 1898.

Salix inquirenda Knowlton, U. S. Geol. Surv. Prof. Paper 140*a*, p. 32, pl. 11, figs. 1, 2, 1926.

Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 168, pl. 47, fig. 10, 1937 (see synonymy).

Salix coalingensis Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 78–79, pl. 7, fig. 6 only, 1930.

Salix sp. Condit, Carnegie Inst. Wash. Pub. 476, V, p. 254, 1938.

Juglans oregoniana Lesquereux. Condit, Carnegie Inst. Wash. Pub. 476, V, p. 257, 1938.

Salix hesperia (Knowlton) Condit. Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

Brown (1937, p. 168) synonymized *Salix inquirenda* and *Juglans hesperia,* as well as several other species. Since *Juglans hesperia* is the older name, this new combination is made: *Salix hesperia.* The Neroly species listed in the synonymy above are now considered to belong here.

An examination of the modern willow leaves in the University of California Herbarium demonstrates that these fossils bear resemblances to *Salix laevigata* Bebb and *S. lasiandra* Bentham. The likeness to the latter is best, including the following characters: numerous fine, sharply pointed teeth, a short petiole, a stout midrib, and only slight difference in size between the tertiary veins and nervilles. The only difference is that the secondary veins are less closely spaced in the fossils. In this character, the fossils are more like the other living species mentioned. Almost all the fossil leaves are large, and large leaves appear to occur more commonly in *Salix lasian-*

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dra than in *S. laevigata*. The present specimens, indeed, are usually somewhat larger than the types of *S. inquirenda*. Inasmuch as some of the Oakvale specimens are of the same size as the types, and all the characters agree, reference of this material to *S. hesperia* seems justifiable.

Salix lasiandra now occurs on the Pacific coast from Canada to southern California, and eastward to the southern Rocky Mountains and the high plateaus of the southwestern United States. It grows along streams and around pools in sandy and gravelly well drained soil, at elevations of 1000 feet or less at the north end of its range, and more than 8000 feet at the south. The material in the University of California Herbarium indicates that large leaves occur more commonly in the northern and higher parts of its range. Abundant large leaves in the fossil collection suggest that the climate at the time of deposition was similar to that of such areas—that is, moist and cool.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2388; nos. 2387, 2389.

Family JUGLANDACEAE

Juglans pseudomorpha new species

(Plate 4, figures 4, 5)

Description. Fruit globose, slightly flattened on ends; diameter 2.5 cm., length 2.0 cm.; husk missing; surface of nut marked with numerous irregularly vertical ridges and grooves; inner surface of nut deeply irregular; seed lobed to fit irregularities; bilocular.

Discussion. The single specimen representing this species illustrates an unusual type of preservation, in which the shell of the nut is preserved, with a partial cast of the seed inside. In its size, shape, and surface markings, it appears to be intermediate between the living *Juglans californica* Watson and *J. nigra* Linnaeus. It is larger than the former and smaller than the latter, and is more complexly sculptured than the former and less so than the latter. It is more similar, however, to the eastern species.

In the absence of any leaf impressions of walnut at Remington Hill, and since no fruits have been found in association with leaves in other floras, this specimen must be given a new name, although it is probably a representative of one of the previously described fossil leaf species that have been regarded as related to *Juglans nigra*. It is interesting to note that this specimen shows characters suggesting that it is intermediate between the typical black walnut and the living California walnut, as might be expected in view of its associates in the fossil flora.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2390, 2390*a*.

Family FAGACEAE

Quercus douglasoides Axelrod

(Plate 5, figures 6, 7)

Quercus douglasoides Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 198–199, pl. 37, figs. 7–10, 1944 (see synonymy and discussion).

Numerous specimens in the flora are exactly like the type of this species. They resemble to some degree the fossils recognized as *Quercus lakevillensis* Dorf and

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Q. payettensis Knowlton, but differ in several constant characters. They are less broad than the former species and broader than the latter, and have peculiar lobes with the top margin normal to the midrib, which gives a stepped effect to the outline of the leaf. These differences appear to be generally consistent also in the similar living species. *Quercus douglasii* Hooker and Arnott is commonly found in the Upper Sonoran zone in California.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2391, 2392.

Quercus prelobata new species

(Plate 7, figures 3, 4)

Description. Leaves pinnately parted into 3 or 4 lobes, the lobes slender, pointed, and entire, or broadened, blunt, and with minor lobes; length 5.5 to 9.0 cm., width 2.7 to 4.4 cm., greatest width across the lobes just below the terminal lobe; base acute to cuneate; alternate or subopposite secondaries diverging from the midrib at angles of 30° to 60°, the angles fairly constant in individual leaves; tertiaries obscure, apparently somewhat percurrent, forming a quadrangular mesh; margins entire or with small minor lobes; texture medium.

Discussion. Fossils representing this species are extremely common at Remington Hill, and were also collected at Oakvale Mine. Among the many specimens seen, all variations in leaf shape present in the living *Quercus lobata* Née were noted, and some going into the range of *Q. garryana* Douglas. The fossil and living species are no doubt closely related. *Quercus lobata* is typical of the inner valleys of California, but may extend as high as 5000 feet in valleys and canyons where ground water is abundant throughout the year.

Although *Quercus moragensis* Axelrod also resembles the leaves produced by the living *Q. lobata,* the Mulholland species differs from the Remington Hill in its consistently smaller size.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2393, 2394; no. 2395.

Quercus pseudo-lyrata Lesquereux

(Plate 8, figures 1, 3)

Quercus pseudo-lyrata Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 8, pl. 2, figs. 1, 2, 1878. Proc. U. S. Nat. Mus., vol. 11, p. 17, pl. 10, figs. 1–3; pl. 11, fig. 1 only; pl. 12, 1888.

Knowlton, U. S. Geol. Surv. Bull. 204, p. 48, 1902.

Chaney, Jour. Geol., vol. 26, p. 582, fig. 2, 1918. Contr. Walker Mus., vol. 2, no. 5, p. 167, 1920. Rept. 28 of State Mineralogist, Calif. Div. Mines, fig. 2, 1932.

Oliver, Carnegie Inst. Wash. Pub. 455, I, p. 20, pl. 5, fig. 4, 1934.

LaMotte, Carnegie Inst. Wash. Pub. 455, V, pp. 121–122, 1936.

Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 172, pl. 50, figs. 7, 8, 1937.

Excellent specimens showing a wide range of variation represent leaves of this species at both localities. The specimen illustrated on plate 8, figure 1, is the same one figured by Chaney in 1932 with the tip added by means of a reversed print of the counterpart. As is indicated by the name, this species was originally considered to be related to one of the lyrate-leafed oaks of eastern United States, probably *Quercus lyrata* Walters. Chaney recognized the relationship of this species to the

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living *Q. kelloggii* Newberry, a conclusion further substantiated by Oliver and LaMotte. Examination of material in the University of California Herbarium shows the following differences between *Q. lyrata* and *Q. kelloggii:* The former has longer lobes and extremely narrow sinuses; the ends of the lobes are rounded rather than pointed, and usually lack a spine; the margins have fewer teeth or subsidiary lobes; and in general, the lamina is longer and narrower than in *Q. kelloggii*. Some of the specimens referred to *Q. pseudo-lyrata,* notably the one from the Blue Mountains of Oregon by Oliver, and that figured on plate 50, figure 7, by Brown, are very similar to *Q. lyrata* and other eastern oaks. The specimen reported by LaMotte from Upper Cedarville is too fragmentary to permit exact comparison, but also appears to be close to the eastern oaks. The majority of the others are intermediate between the two living oaks here discussed, although some, such as those figured by Lesquereux (1888) on plate 10, figure 3, plate 11, figure 1, and plate 12, and by Chaney (1918) from the Eagle Creek flora closely approach many leaves of *Quercus kelloggii*. The Oakvale Mine specimens and many of those at Remington Hill are practically indistinguishable from typical leaves of the California black oak.

Although the extreme forms of this species, the Oakvale Mine specimens and those reported by Oliver and Brown, might be regarded as separate species, the presence of a continuous series of intermediate forms clearly shows that all may be referred to a single fossil species. Knowlton mentioned that he arranged about 100 specimens from the John Day Basin in a series and was unable to separate them into different species. The existence of this series is apparent even in the relatively few published illustrations, and a large part of it is represented by the fossils found at Remington Hill. During a recent trip to Oakvale Mine and Remington Hill, the writer collected leaves of *Quercus kelloggii* and found specimens which matched all the fossils that have been assigned to *Q. pseudo-lyrata,* even the extreme forms represented by Oliver's and Brown's specimens. Thus the evidence of both the fossil and the modern leaves verifies the identification of all the leaves referred to *Q. pseudo-lyrata,* and strongly indicates that they are closely related to the living *Q. kelloggii.*

The California black oak is distributed from southwestern Oregon through California almost to the Mexican border, at elevations from 1500 feet at the north to 7000 feet at the south. It is best developed in the Transition zone, but overlaps into the upper part of the Upper Sonoran zone. It is not limited to stream borders, but is found widespread throughout its range.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2396, 2396*a* (counterpart), 2397.

Quercus remingtoni new species

(Plate 6, figures 1–3, 5–7; plate 7, figures 1, 2; plate 8, figure 2)

Description. Leaves highly variable in shape, ranging from obovate to lanceolate or oblanceolate; 4.3 to 8.3 cm. long and 1.3 to 4.4 cm. wide; apex spinose, rounded or acute in broader leaves, acute to acuminate in the lanceolate forms; base rounded, usually asymmetrical in the broad leaves, symmetrical in the lanceolate; petiole 0.5 to 1.7 cm. long; midrib stout in most leaves, somewhat wavering in the upper half of broad leaves; 4 to 8 pairs of alternate to subopposite secondaries, the basal 3 or 4 leaving the midrib at angles of 50° to 80°, the upper ones at 20° to 35°; the 4th or 5th pair in the broader forms longer and stronger than the others, reaching upward and outward to very large teeth or small, blunt lobes; tertiaries irregularly percurrent;

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nervilles forming a fine angular mesh; margin entire for a short distance from the base, becoming sinuate-serrate or serrate, rarely dentate, with spine-tipped teeth; the teeth ranging from moderate-sized, sharply serrate or sinuate-serrate in lanceolate leaves to large, strongly sinuate-serrate in broad leaves, even forming short lobes in the latter; texture thick.

Discussion. A large number of leaves in the Remington Hill deposits represent this species. As judged from material in the University of California Herbarium, *Quercus morehus* Kellogg most closely matches the fossils. This living species is similar to *Q. remingtoni* in the following characters: the size and proportions of the leaves; teeth with convex lower side and sharply curved sinus above; the upward-pointing spine; the rounded base; the varying apices; and the angles of the secondaries with the midrib. The variation of the fossils from obovate, lobate shape to lanceolate, toothed shape is within the range found in *Q. morehus,* as seen on University of California Herbarium sheets 527687, 569825 (lobate form), 5656, 186589, 549114 (lanceolate form).

Objection to this suggested relation may be made on the ground that *Q. morehus* is a hybrid, and not possibly a descendant of *Q. remingtoni.* It may be suggested that it is possible for a hybrid comparable with the living *Q. morehus* to have existed in the past, and to be represented by leaves now called *Q. remingtoni.* This suggestion acquires support when it is realized that *Q. pseudo-lyrata,* an ancestor of *Q. kelloggii* Newberry, which is one of the parents of *Q. morehus,* is frequently found in association with *Q. remingtoni* in the flora. Furthermore, several of the fossils represent *Q. wislizenoides,* which is related to leaves of the living *Q. wislizenii* A. DeCandolle, the other parent of *Q. morehus.*

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2398, 2399, 2400, 2401, 2402, 2403, 2404, 2405, 2406.

Quercus simulata Knowlton

(Plate 5, figure 3)

Quercus simulata Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 728, pl. 101, figs. 3, 4; pl. 102, figs. 1, 2, 1898.
MacGinitie, Carnegie Inst. Wash. Pub. 416, II, p. 53, pl. 6, fig. 2, 1933 (see discussion).
Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 173, pl. 50, fig. 1, 1937 (see synonymy).

Several specimens collected at Remington Hill appear to be identical with *Quercus simulata.* One partially preserved leaf (no. 2392) from Oakvale Mine can be doubtfully identified as being of the same species. The modern equivalent of *Q. simulata* is *Q. myrsinaefolia* Blume of eastern Asia.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2441; no. 2442.

Quercus winstanleyi Chaney

(Plate 5, figure 2)

Quercus winstanleyi Chaney, Carnegie Inst. Wash. Pub. 553, pp. 342–345, pl. 60, figs. 1, 3–5; pl. 61, figs. 1, 2, 4; pl. 62, fig. 2, 1944.

A typical leaf of this species, which is especially abundant in the Pliocene flora at Troutdale, Oregon, is represented in the collections. On the basis of the material which has been studied by Chaney, this species is considered to be related to *Quercus*

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aliena Blume of central and western China, and *Q. prinus* Linnaeus of the eastern United States.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2407.

Quercus wislizenoides Axelrod

(Plate 5, figures 4, 5)

Quercus wislizenoides Axelrod, Carnegie Inst. Wash. Pub. 553, p. 136, pl. 29, figs. 4–9, 1944 (see synonymy).

Five leaves are referred to this species, which shows relationship to the living *Quercus wislizenii* A. DeCandolle of California. The fossil leaves are somewhat more slender than the large, long-lanceolate leaves commonly produced by the interior live oak, but otherwise they closely resemble it. The Remington Hill fossils are larger than those figured by Axelrod from the Mulholland and Oakdale floras. This is presumably a reflection of the more mesic habitat at Remington Hill. The modern *Q. wislizenii* produces larger leaves in areas where it meets the redwood forest than in drier situations in the interior and to the south.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2447, 2448; no. 2449.

Acorn

(Plate 6, figure 4)

Several acorns are preserved, with heavy carbonaceous deposits in the impressions, but their relationships are unknown.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2436.

Family ULMACEAE

Ulmus californica Lesquereux

(Plate 8, figure 4)

Ulmus californica Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. *7a,* 1878.

Ulmus affinis Lesquereux, *ibid.,* p. 16, pl. 4, figs. 4, 5.

Several leaves in the collections are closely similar to those produced by the living *Ulmus americana* Linnaeus on the drier borders of its distribution at the west. The fossil species is now known to survive into the Lower Pliocene of California.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2409; no. 2408.

Family BERBERIDACEAE

Mahonia malheurensis Arnold

Mahonia malheurensis Arnold, Contr. Mus. Paleontol. Univ. Mich., vol. 5, no. 4, p. 63, pl. 3, figs. 1–3, 1936.

Several specimens of this species were collected at Remington Hill, all in a single block about 2 inches thick and less than a foot in diameter. They are of

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about the same size as the type specimens from Succor Creek and Trout Creek. Comparison with modern members of this genus in the University of California Herbarium indicates that the fossils are most similar to the longer leaflets of *Mahonia haematocarpa* (Wooton) Fedde, an evergreen shrub growing on the lower slopes of the mountains in southern Arizona and New Mexico.

Vauquelinia angustifolia Rydberg shows some resemblance to the Remington Hill fossils, and a very marked likeness to the types illustrated by Arnold. This Mexican *Vauquelinia* has a long, slender leaf of uniform width for most of its length, whereas the Mahonias resembling the fossils tend to have a broader leaf with a long, slender terminal lobe. In *Vauquelinia* the teeth are small and relatively numerous, whereas in *Mahonia* they are large and few. *Vauquelinia* has a short, acute apex, not much above the last pair of teeth, but *Mahonia* may have almost half the length of the leaf between its tip and the last teeth. The secondary veins in *Vauquelinia,* as in the Succor Creek and Trout Creek leaves, are long and depart from the midrib at angles of about 10°, going straight for most of their length, then turning into the teeth at about 30°; *Mahonia* does not have long, straight secondaries like this, but has characteristic looping veins leaving the midrib at angles of 30° to 60°. In *Vauquelinia,* some of the branches of the secondaries loop in a *Mahonia*-like way, but do so much less conspicuously.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2410, 2411.

Family LAURACEAE

Persea pseudo-carolinensis Lesquereux

Persea pseudo-carolinensis Lesquereux (in part), Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 19, pl. 7, fig. 2 (not fig. 1, which is *Magnolia californica* Lesquereux), 1878.

This species was evidently rare in the Remington Hill community, inasmuch as it is represented by only a single leaf. Considering the durable nature of the leaves of the related modern species, *Persea borbonia* Sprengel, and the probable durability of the fossil leaves, it is likely that if they had been abundant, more of them would have been preserved. The scarcity of this species may be due to the elevation at which the fossils were deposited, since the modern *P. borbonia* is more or less closely restricted to the lowlands.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2412.

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939 (see synonymy).

Several leaves in the collections from Oakvale Mine and Remington Hill appear to represent this species. An impression of a fruit of *Umbellularia,* with a thick carbonaceous film surrounding an impression of the stone, was collected from Oakvale Mine. Wood sections from Oakvale Mine have been identified by Lyman H. Daugherty, of San Jose State College, as *Umbellularia. Umbellularia salicifolia* has been compared with *U. californica* Nuttall, a tree or large shrub common in the Coast Ranges of southern Oregon and California, ranging from a rainy climate in the north to a dry climate in the southern California hills. In the north it is commonly large, but in the south it is more often a small tree or shrub, and is restricted

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to gullies and canyons where ground water is available throughout the year. It also occurs on the lower slopes of the Sierra Nevada from Shasta County southward, in the Upper Sonoran and Transition zones.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2413, 2414, 2415.

Family HAMAMELIDACEAE

Liquidambar pachyphyllum Knowlton

(Plate 10, figure 1)

Liquidambar pachyphyllum Knowlton, U. S. Geol. Surv. Bull. 204, p. 63, pl. 9, fig. 1, 1902.
U. S. Geol. Surv. Prof. Paper 140*a*, p. 42, pl. 22, fig. 7; pl. 29, fig. 1, 1926.
Chaney, Contr. Walker Mus., vol. 2, no. 5, p. 174, pl. 15, figs. 2, 3, 1920.

Liquidambar europaeum patulum Knowlton, U. S. Geol. Surv. Bull. 204, p. 62, pl. 10, fig. 5, 1902.

Liquidambar sp. ? Knowlton, U. S. Geol. Surv. Bull. 204, p. 63, pl. 12, fig. 4, 1902.

Liquidambar acutilobum Chaney, Contr. Walker Mus., vol. 2, no. 5, p. 175, pl. 15, fig. 4, 1920.

The Remington Hill specimens of *Liquidambar* were found only in sandy layers, with consequent poor preservation. Nevertheless, in the several specimens collected there is sufficient detail to indicate clearly their relationship to both *L. pachyphyllum* and the modern *L. styraciflua* Linnaeus.

According to MacGinitie (oral communication, June 1940), the Eocene *L. californicum* Lesquereux is distinct from the Miocene and Pliocene *L. pachyphyllum*. Berry has synonymized the Middle Tertiary Liquidambars of the western United States with *L. californicum* (1929, p. 250), and considers that they represent one species. *Liquidambar pachyphyllum* can be distinguished from *L. californicum*, however, by its deep sinuses and slender lobes; *L. californicum* has relatively rounded lobes separated by shallow sinuses. There is no evidence of any gradation between these two forms, as suggested by Berry. A consideration of the figured specimens cited by him (*loc. cit.*) shows that Lesquereux's types of *L. californicum* from Chalk Bluffs have rounded, shallow lobes; all the other figures are of the *L. pachyphyllum* type, with the exception of two figures from Bridge Creek (Newberry, 1898, pl. 47, figs. 1, 2). Under these circumstances, it seems best to retain *L. californicum* and *L. pachyphyllum* as separate species.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2416.

Family PLATANACEAE

Platanus paucidentata Dorf

(Plate 9; plate 10, figure 4; plate 11, figure 5)

Platanus paucidentata Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 94–96, pl. 10, figs. 4, 9; pl. 11, fig. 1; pl. 12, fig. 1, 1930.
Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 174–175, pl. 5, figs. 4, 5, 1937.

A large suite of fossils from Remington Hill and Oakvale Mine represent this species. Variations are found ranging from almost unlobed leaves to those with deep sinuses and narrow lobes. Specimens representing almost all gradations between

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toothed and entire margins are present in the collections. It is believed that the Remington Hill fossils represent a single species.

The fossil leaves resemble those of the living California sycamore, *Platanus racemosa* Nuttall.

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2417, 2418, 2419.

Family ROSACEAE

Crataegus newberryi Cockerell

(Plate 11, figures 1–3)

Crataegus newberryi Cockerell, Univ. Colo. Studies, vol. 5, p. 43, 1908.
Chaney, Carnegie Inst. Wash. Pub. 346, IV, pp. 121–122, pl. 14, figs. 6, 10, 1927.
LaMotte, Carnegie Inst. Wash. Pub. 455, V, p. 131, 1936.
Crataegus flavescens Newberry, Proc. U. S. Nat. Mus., vol. 5, p. 507, 1883. U. S. Geol. Surv. Mon. 35, p. 112, pl. 48, fig. 1, 1898.

Four specimens of *Crataegus* are near the lower size limit of the types from Bridge Creek, and the lobes also have lower angles of divergence. Comparison of these fossils with herbarium material shows similarity to *C. cuneata* Siebold and Zuccarini, found in central China at elevations ranging from 500 to more than 5000 feet. With a fuller representation, however, Chaney found that this species was most closely matched by *C. pinnatifida* Bunge, an inhabitant of northern China, eastern Siberia, and Korea. It lives in a cool, moderately dry climate at middle elevations. The Remington Hill fossils are also close to the smaller leaves of *C. pinnatifida* (see University of California Herbarium sheet 236231).

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2420, 2421, 2422.

Prunus petrosperma new species

(Plate 10, figure 2)

Description. Seeds 1.0 to 1.5 cm. in diameter, present thickness less than 0.5 cm.; flattened by crushing; surface marked with one deep groove extending from proximal end toward distal end, and with minor interlacing ridges over the surface branching from the groove and from the end.

Discussion. Three seed casts and a mold show the characters noted above, and appear to have been very much like the seeds of *Prunus ilicifolia* Walpers before they were crushed by the sediments in which they were buried. No trace of the flesh that once surrounded the seeds now remains. *Prunus ilicifolia* is an evergreen shrub or small tree common on slopes and valleys from 100 to 4000 feet in elevation, in the Coast Ranges of middle California and southward discontinuously to Baja California, with a variety on the Channel Islands off the southern California coast. It will grow in dry soil, but does better in areas where ground water is abundant.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2423.

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Family ACERACEAE

Acer negundoides MacGinitie

Acer negundoides MacGinitie, Carnegie Inst. Wash. Pub. 416, II, p. 62, pl. 11, figs. 2, 3, 1933.

Chaney, Carnegie Inst. Wash. Pub. 476, IV, p. 216, pl. 6, fig. 2; pl. 7, figs. 1*a*, 1*b*, 1938.

This species is represented only by fruits in the Remington Hill collections. It has been reported several times in Upper Miocene or Lower Pliocene floras of northwestern North America, and is usually represented by seeds with few if any leaves associated.

As the name indicates, the fossil species is closely allied to the living *Acer negundo* Linnaeus, which is widely distributed throughout North America, in many types of climate. The eastern varieties are subject to moist climates with moderately cold winters; the California variety, *A. negundo* var. *californicum* Sargent, is capable of withstanding considerable drought in the summer, although in general found along watercourses; the southwestern variety is restricted to watercourses in a climate marked by deficient rainfall and wide temperature ranges. It is impossible to relate the fossils to any one of these varieties, but it may be said that the fossils resemble the southwestern variety less than the others.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2424, 2425.

Family HIPPOCASTANACEAE

Aesculus preglabra new species

(Plate 10, figure 3; plate 11, figures 4, 6)

Description. Leaflets obovate, tip acute, base long cuneate; 8.0 to 10.0 cm. long, 2.5 to 4.0 cm. wide; petiole missing; midrib thin, slightly curved; secondary veins 5 mm. apart, opposite or subopposite, leaving midrib at angles of 80° near base and 40° near tip, camptodrome close to margin; tertiary veins scattered, irregularly percurrent, usually normal to secondaries; veinlets very small, reticulate; margin entire near the base, finely serrate in middle and tip of leaflet, occasional teeth larger than others; texture thin.

Discussion. *Aesculus* leaflets are rare in the fossil record. These specimens, however, show characters which strongly suggest that they belong to this genus. They are to be distinguished from *Carya* leaflets on the basis of the rarity or absence of craspedodrome branches at the ends of the secondaries, the shape of the base, and the straightness of the basal secondaries. They do not resemble any other fossil species of *Aesculus* with which the writer is familiar. Among living species, *A. glabra* Willdenow, as shown on University of California Herbarium sheets 67653 and 377441, resembles the fossils most closely. This species is a small tree or shrub occurring along creeks and on hillsides from the western slopes of the Appalachians to Kansas, Nebraska, and Oklahoma, but is nowhere abundant.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2426, 2427, 2428.

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Family SAPINDACEAE

Ungnadia clarki new species

(Plate 12, figures 1, 6, 7)

Description. Leaflets lanceolate, base rounded or cuneate, tip acuminate; length preserved 5 to 7 cm., width 2 to 3 cm., maximum width about ⅓ to ¼ of the distance above the base; petiolule usually absent, the leaflets apparently sessile; midrib straight or slightly curved, thick, apparently persisting to the tip; secondaries 8 to 12 pairs, opposite or subopposite in proximal part, alternate in distal part of lamina, leaving midrib at angles varying from almost 90° in the basal pair to 45° in the distal pair, nearly straight at the base, evenly curved toward the apex in distal part of lamina; tertiaries irregularly percurrent, on the average about 2 to 3 mm. apart, those near the margin thicker, forming successive loops to the next higher secondary, with branches running toward the teeth; nervilles obscure; margin serrate, with moderately coarse teeth, to which the veins occasionally extend; more commonly, however, the veins extend toward the sinus, lying directly above the tooth; texture thin.

Discussion. An examination of fossil and living material of various woody plants shows that these impressions bear a resemblance to several different genera. Certain species of *Fraxinus, Amelanchier, Planera,* and *Zelkova* are somewhat similar in foliage. The nervation and the margins of these genera differ from those of the present fossils, whereas the leaflets of *Ungnadia speciosa* Endlicher are separated from them by only one unimportant character. This discrepancy is in the tertiary nervation, which is slightly more regularly percurrent in the fossils than in the leaflets of the living tree. Even this difference disappears when comparisons are made with some of the specimens in the University of California Herbarium. One other genus, *Koelreuteria,* has foliage which approaches the fossils very closely. The leaflets of this genus differ from the fossils in the following respects: the teeth are more numerous and closer together; the secondary veins are closer together and are straighter near the midrib; the basal secondaries do not show a reverse curve. The characters of the fossils suggest that they are related to *Ungnadia* rather than to any of the other genera mentioned. This conclusion is supported by the presence in the collection of an impression of what is apparently a three-parted thick-walled capsule. This may well represent the capsule of *Ungnadia,* buried after the seeds had been shed.

Ungnadia has never before been reported in the fossil record, but certain leaf impressions from various horizons in North America are similar to these fossils in many ways. *Fraxinus eocenica* Lesquereux (1878*b*, p. 229; 1883, p. 123, pl. 20, figs. 1–3) from Golden, Colorado, is similar in all respects except that it has a cuneate base and fewer secondaries. The specimen of this species figured by Knowlton (1930, pl. 52, fig. 4) appears to be identical with the Oakvale Mine specimens. *Ulmus tenuinervis* Lesquereux from Florissant beds (1878*b*, p. 188, pl. 26, figs. 1–3) has a similar shape and venation, except that the secondaries are more curved. The margin, however, is quite different, having many more and much smaller teeth. *Planera inequilateralis* (Lesquereux) Knowlton from the Green River (see Newberry, 1898, p. 34, pl. 66, fig. 6) has the appearance of terminal leaflets of *Ungnadia,* but has smaller and fewer teeth. *Aralia triloba* Newberry from the Dakota beds at Fort Clark (1898, p. 123, pl. 40, figs. 4, 5) is similar to the fossils in this collection except for larger and more numerous teeth. The illustrations of this *Aralia* suggest that its leaves are divided into leaflets; if this is not the case, the similarity to *Ungnadia* dis-

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appears. *Cupanites formosus* Berry, from the Wilcox (1930*a*, p. 98, pl. 30, fig. 2), differs from *Ungnadia* in having the basal veins at a sharper angle with the midrib, asymmetrical bases, and cuneate bases on the lateral leaflets, although otherwise it is similar. No fossils of the late Tertiary that the writer has seen are at all similar to the present specimens. In view of the present distribution and climatic requirements of *Ungnadia,* its presence in the later and more arid floras is to be expected.

Ungnadia speciosa is found in northern Mexico and southwestern United States. It is a stream-border tree throughout much of its range, although it is also found on hillsides and open slopes. It ranges in elevation from near sea level to nearly 6000 feet. A sheet in the University of California Herbarium records its occurrence in the Organ Mountains, New Mexico, at 5800 feet. MacGinitie (oral communication, June 1939) reports that he has seen it south of Monterrey, Mexico, at about 3000 feet, where it was the dominant, in association with sycamore, grape, box elder, and large-leafed willow, in a region with 50 or 60 inches of rainfall yearly.

This species is named in honor of Dr. Bruce L. Clark, of the Department of Paleontology at the University of California.

Occurrence. Oakvale Mine, loc. 204.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2429, 2430, 2431.

Family RHAMNACEAE

Berchemia multinervis (Al. Braun) Heer

(Plate 12, figure 4)

Berchemia multinervis (Al. Braun) Heer, Flora tertiaria Helvetiae, vol. 3, p. 77, pl. 123, figs. 9–18, 1859.
Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 7, p. 277, pl. 52, figs. 9, 10, 1878.
Knowlton, U. S. Geol. Surv. Prof. Paper 101, p. 333, pl. 101, fig. 5, 1917.
MacGinitie, Carnegie Inst. Wash. Pub. 465, III, pp. 145–146, pl. 13, fig. 1, 1937.
Condit, Carnegie Inst. Wash. Pub. 476, V, p. 265, 1938.

The genera *Karwinskia* and *Berchemia* have leaves which are extremely difficult to distinguish from each other when detached from the plant. No character is consistently present in one genus and consistently absent from the other, although a few minor characters commonly occur in the leaves of one and but rarely in those of the other. The difficulty of separating these genera is increased when one is dealing with fossil leaves. Several leaves in the collection from Oakvale Mine present this problem. Among these, one almost exactly matches leaves of *Berchemia scandens* Trelease, on University of California Herbarium sheet 80225 from Lake County, Florida; another is even more closely matched by leaves of the same species from Houston, Texas, on sheet 426179. No leaves of *Karwinskia* in the University of California Herbarium are so closely similar to the fossils as are those of *Berchemia,* and in general, *Karwinskia* leaves when mature are larger and somewhat narrower in proportion to length than are either the fossils or living *Berchemia* leaves. Thus, such evidence as is available, though not decisive, lends its weight to the determination of these fossils as *Berchemia.*

As the plant fossil record becomes more and more complete, one may expect to find cases in which two or more modern, closely related genera have differentiated from a single Tertiary ancestor, so that the fossil cannot be considered to be related to one of the modern genera exclusively. These fossils may be an example of this situation. *Karwinskia* and *Berchemia* are very similar in all structures. According to Small

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(1913, p. 749), the differences in fruiting structures are matters of degree rather than kind. In *Berchemia,* for instance, the ovary is half immersed in the disk, whereas in *Karwinskia* it is wholly immersed. There are other lesser differences, such as the shape of the petals and the organization of the inflorescence. The difference in habit is suggestive: *Karwinskia* is a shrub, whereas *Berchemia* is a climbing vine, a more common habit in a dense humid-climate forest.

The presence of *Berchemia* or of a *Berchemia*-like plant in the Arcto-Tertiary Flora is recorded by leaf impressions associated with other plants which indicate a temperate, humid type of climate similar to that in which *Berchemia* now thrives. The habit of this plant may have been like that of the living *Berchemia,* because light would be at a premium in its habitat. By Miocene time, under the influence of the increasingly rigorous climate developing in parts of western North America, a section of this genus may have become adapted to more arid conditions. Living in a thinner forest, this group of plants may have developed a more compact habit. Such changes in tolerance and habit, and small alterations in the fruit organs, would result in a plant like *Karwinskia.* Such a plant could appear in the Middle Miocene Tehachapi flora of southern California. In other parts of North America, and also eastern Asia, where the climate remained more humid, *Berchemia* remained relatively unchanged, as its occurrence in the Mio-Pliocene Neroly flora of central California indicates (Condit, 1938, p. 265). In the western United States, with the extension of more or less arid conditions in the Pliocene, *Berchemia* was exterminated, surviving in the eastern part of the continent, where aridity did not develop. *Karwinskia,* which was more suited to aridity, is now common in the southwestern United States and northern Mexico.

The precise place of the Oakvale Mine fossils in this suggested historical series is uncertain, but, as was pointed out above, the evidence suggests that these fossils are to be considered *Berchemia* rather than *Karwinskia.*

Occurrence. Oakvale Mine, loc. 204; Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2432; no. 2433.

Ceanothus precuneatus Axelrod

Ceanothus precuneatus Axelrod, Carnegie Inst. Wash. Pub. 516, p. 120, pl. 11, fig. 7, 1939.

The single specimen is not well preserved as to details of venation, but the shape and margin are characteristic of species of *Ceanothus.* The only argument against this identification is the fact that the secondaries in the fossil are poorly preserved, whereas in the living species of *Ceanothus* which it resembles the secondaries are large and should leave impressions in the matrix. When the fossil was uncovered, a thick carbonaceous film was present in which faint ridges suggestive of secondary veins were noted. This film was largely destroyed before the specimen could be prepared in the laboratory.

The fossil closely resembles *Ceanothus cuneatus* Nuttall, a species widespread in the Upper Sonoran and Transition zones from Oregon to Baja California, and commonly found on rocky, exposed hillsides. It also bears close likeness to *C. rigidus* Nuttall var. *grandifolius* Torrey, a species related to *C. cuneatus* which is found in the Coast Ranges of California from the northern shore of San Francisco Bay southward for about a hundred miles.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2434.

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Family VITACEAE

Vitis bonseri Berry

(Plate 12, figure 5)

Vitis bonseri Berry, U. S. Geol. Surv. Prof. Paper 170*c*, p. 41, pl. 13, fig. 6, 1931.

One specimen and its counterpart from Remington Hill appear to be identical with the seed impression described by Berry from Grand Coulee. As he states, the fossils resemble many living species of *Vitis*. Brown (1937*a*, p. 182) suggests that the seed and the leaves named *Vitis washingtonensis* (Knowlton) Brown may represent the same species, and figures a leaf of *Vitis cordifolia* Michaux similar to the fossil leaves. The writer does not, however, believe that a definite statement regarding the relationships of *Vitis bonseri* can yet be made.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2435, 2435*a* (counterpart).

Family ERICACEAE

Arbutus matthesii Chaney

Arbutus matthesii Chaney (in part), Carnegie Inst. Wash. Pub. 346, IV, pp. 131–132, pl. 20, figs. 1, 5 (not figs. 3, 4, which are *Nyssa elaenoides* (Lesquereux) Condit), 1927.

One nearly complete leaf impression represents this species. The identification is made almost certain by the shape and the nature of the margin, and still more by the peculiar way in which small veins branch from the lower side of the wavering secondaries.

Arbutus matthesii is very similar to *A. menziesii* Pursh, a common tree at middle elevations from British Columbia southward to Baja California. It is commoner in the coastal mountains, where precipitation and sea fogs occur more regularly than in the interior.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2437.

Arctostaphylos martzi new species

(Plate 12, figure 2)

Description. Leaf ovate, base blunt cuneate, tip rounded; 3.0 cm. long, 2.3 cm. wide; petiole missing; midrib straight, slightly curved distally; secondary veins 3 to 4 mm. apart, opposite or subopposite, leaving midrib at angles of about 35°, curved, camptodrome, looping to join those next above; tertiary veins irregularly percurrent, perpendicular to midrib, anastomosing with intersecondary veins, and near the margin forming a subsidiary loop system outside the secondaries; veinlets irregularly and finely reticulate; margin entire; texture coriaceous.

Discussion. The single leaf representing this species in the Remington Hill collections is incompletely preserved, yet details are sufficiently clear to permit the recognition of its relationship to the genus *Arctostaphylos*. Specific relationships are less clear, but it appears to be closest to *A. manzanita* Parry, on account of the presence of tertiary veins lying perpendicular to the midrib.

Arctostaphylos manzanita is found on the northern Coast Ranges of California,

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and on the lower slopes of the Sierra Nevada as far south as Tuolumne County. It is growing today at the fossil locality.

This species is named for Mr. Clarence Martz, of Nevada City, California, who gave valuable assistance in the collection of the flora.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2438.

Family CAPRIFOLIACEAE

Viburnum platyspermum new species

(Plate 12, figure 3)

Description. Seed 1 cm. long, 6 mm. wide, proximal end rounded, distal end bluntly cuneate; two poorly preserved longitudinal ridges extending from distal end downward and disappearing about halfway down the seed.

Discussion. In shape, size, and external markings, this specimen is similar to seeds of *Viburnum ellipticum* Hooker. The chief difference lies in the weaker development of the ridges, which may be due to crushing subsequent to burial. It is probable that the plant from which this seed was derived was a relative of the living *V. ellipticum.*

Viburnum ellipticum is a shrub found in canyons and valleys at elevations of 1000 to 4000 feet in the north Coast Ranges of California, in parts of the northern Sierra Nevada, and northward to Washington.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2439.

INCERTAE SEDIS

Abies ? sp.

A single incomplete needle indicates by the arrangement of the ridges and grooves and the notched tip that it probably represents the genus *Abies.* Specific characters are wholly lacking.

Occurrence. Remington Hill, loc. P3935.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2440.

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PLATES 1—12

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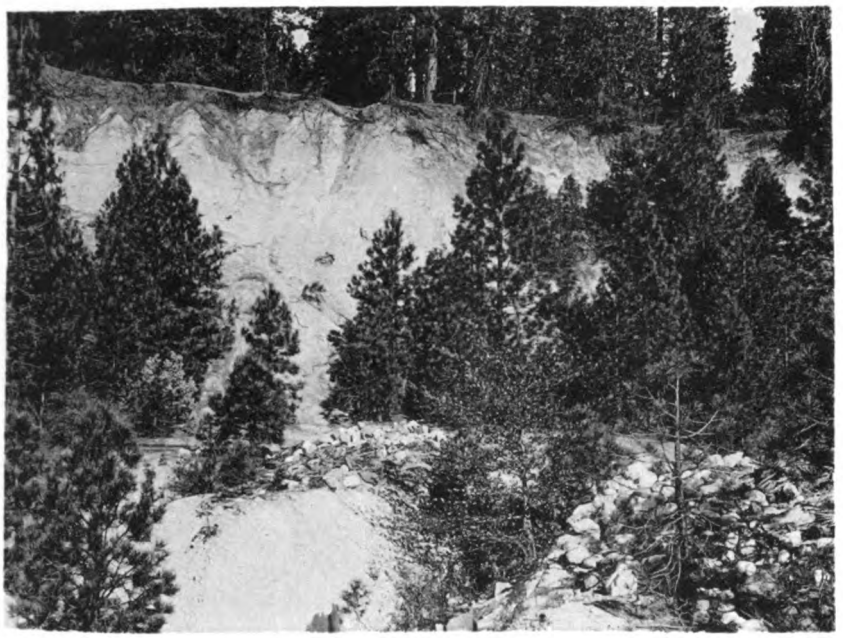

FIG. 1. Remington Hill, locality P3935. Excavation may be noted at center of picture.

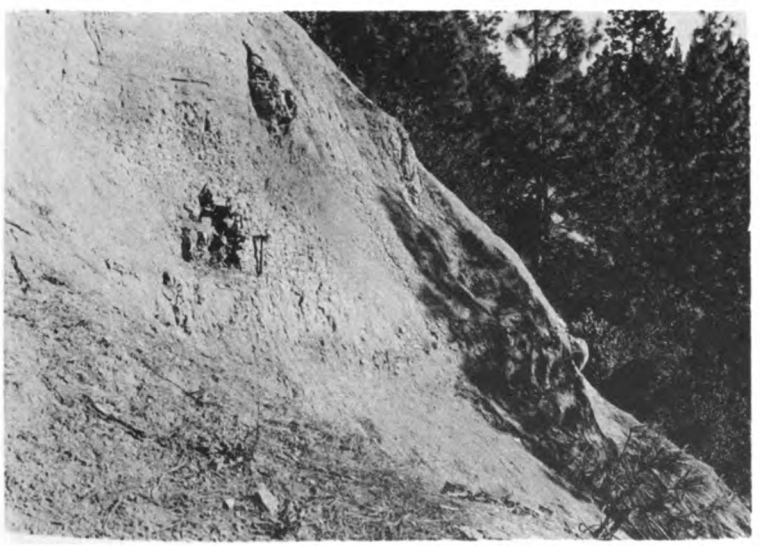

FIG. 2. Closer view of locality P3935

REMINGTON HILL LOCALITY

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FIG. 1. Modern forest on slopes near Remington Hill, with *Pinus ponderosa, Libocedrus decurrens, Abies concolor,* and *Quercus kelloggii.*

FIG. 2. Oakvale Mine, locality 204

REMINGTON HILL LOCALITY AND MODERN VEGETATION

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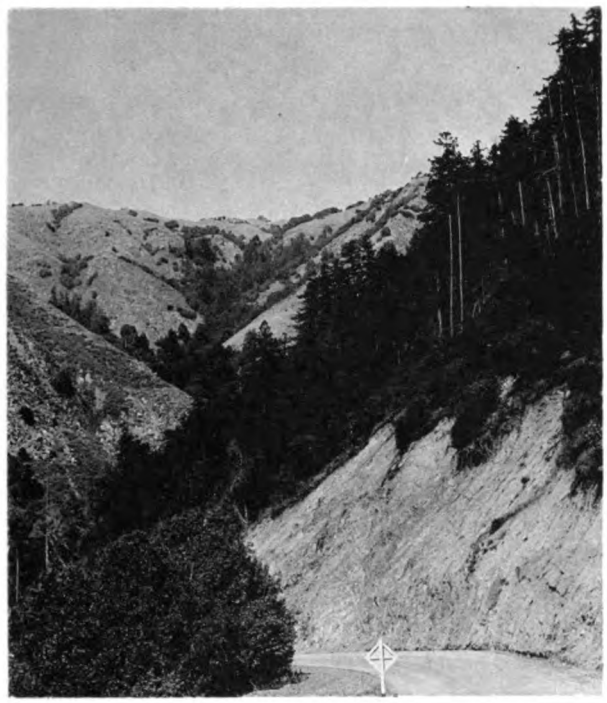

FIG. 1. Redwood and chaparral vegetation near Big Sur, California.

FIG. 2. South side of Carmel Valley, 7½ miles from the ocean, with live oaks on the slopes and groups of redwoods at the mouth of Robisons Canyon (center of picture) and up a side canyon. (Photograph by Laidlaw Williams.)

REMINGTON HILL MODERN EQUIVALENT VEGETATION

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PLATE 4

Remington Hill fossils

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Fig. 1. *Sequoia langsdorfii* (Brongniart) Heer. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2376 39

Fig. 2. *Chamaecyparis gracilis* Condit. Holotype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 2381 39

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Fig. 4. *Juglans pseudomorpha* Condit. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 2390*a*. The interior of the shell, after the removal of the seed . . . 42

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Fig. 7. *Salix hesperia* (Knowlton) Condit. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2388 41

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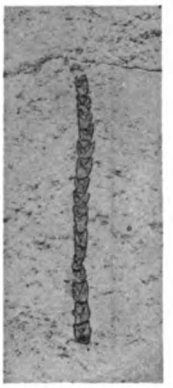

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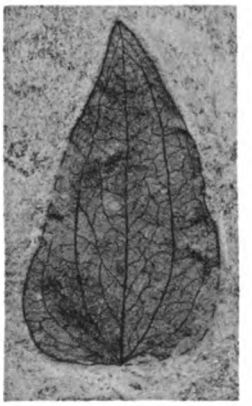

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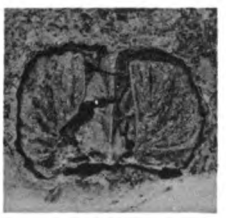

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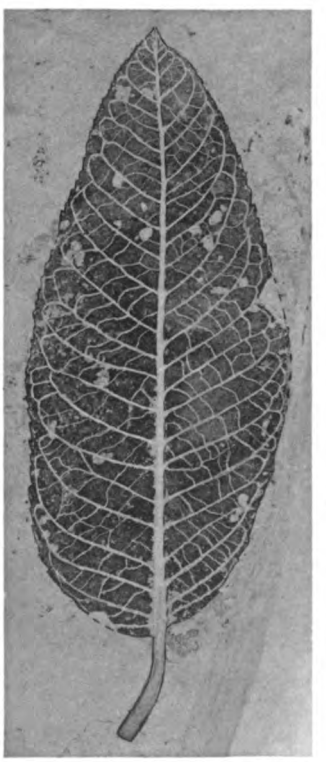

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PLATE 5

Remington Hill fossils

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Fig. 1. *Quercus aliena* Blume. U. C. Herbarium sheet 281368. For comparison with *Quercus winstanleyi*.

Fig. 2. *Quercus winstanleyi* Chaney. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2407 45

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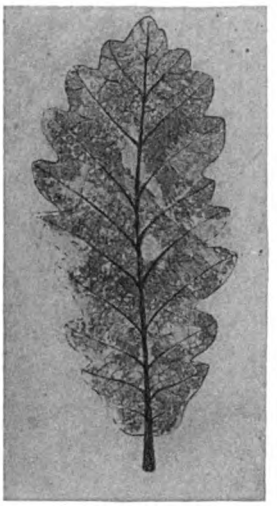

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PLATE 6

REMINGTON HILL FOSSILS

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FIGS. 1–3, 5–7. *Quercus remingtoni* Condit. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2398, 2402, 2403, 2401, 2405, 2406 44

FIG. 4. Acorn. U. C. Mus. Pal., Paleobot Ser., no. 2436 46

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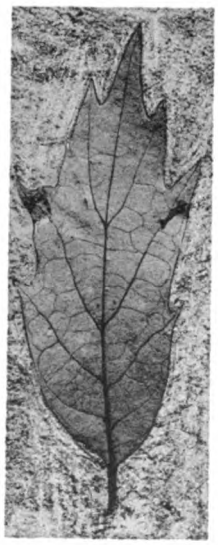

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PLATE 7

REMINGTON HILL FOSSILS

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FIGS. 1, 2. *Quercus remingtoni* Condit. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2399, 2400 44

FIGS. 3, 4. *Quercus prelobata* Condit. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2393, 2394 43

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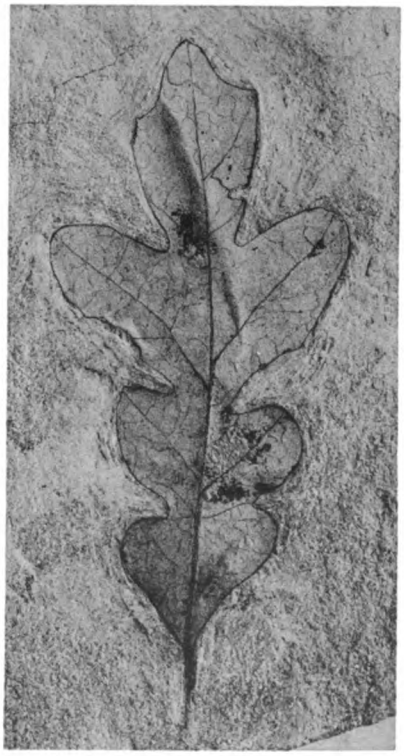

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PLATE 9

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Platanus paucidentata Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2417 48

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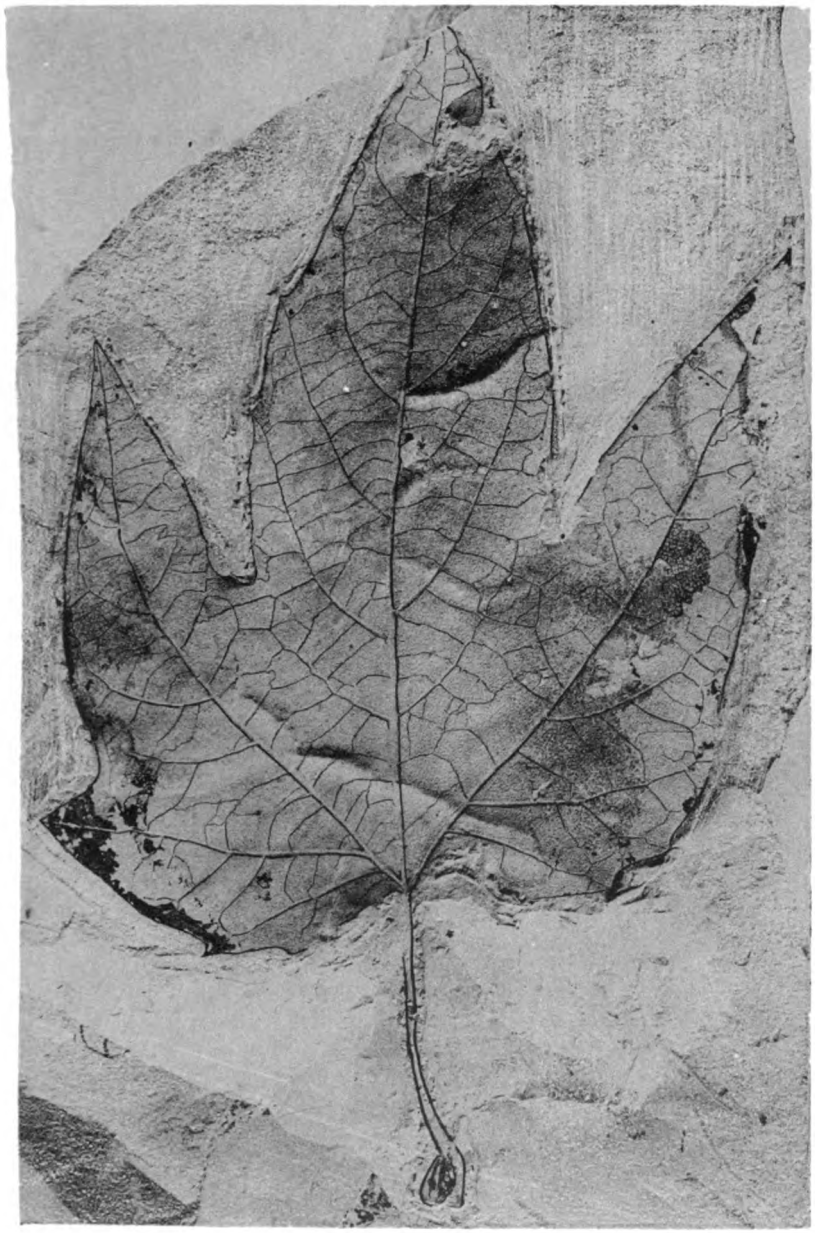

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PLATE 10

Remington Hill fossils

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Fig. 1. *Liquidambar pachyphyllum* Knowlton. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2416 48

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Fig. 4. *Platanus paucidentata* Dorf. Plesiotype. × 0.5. U. C. Mus. Pal., Paleobot. Ser., no. 2418 48

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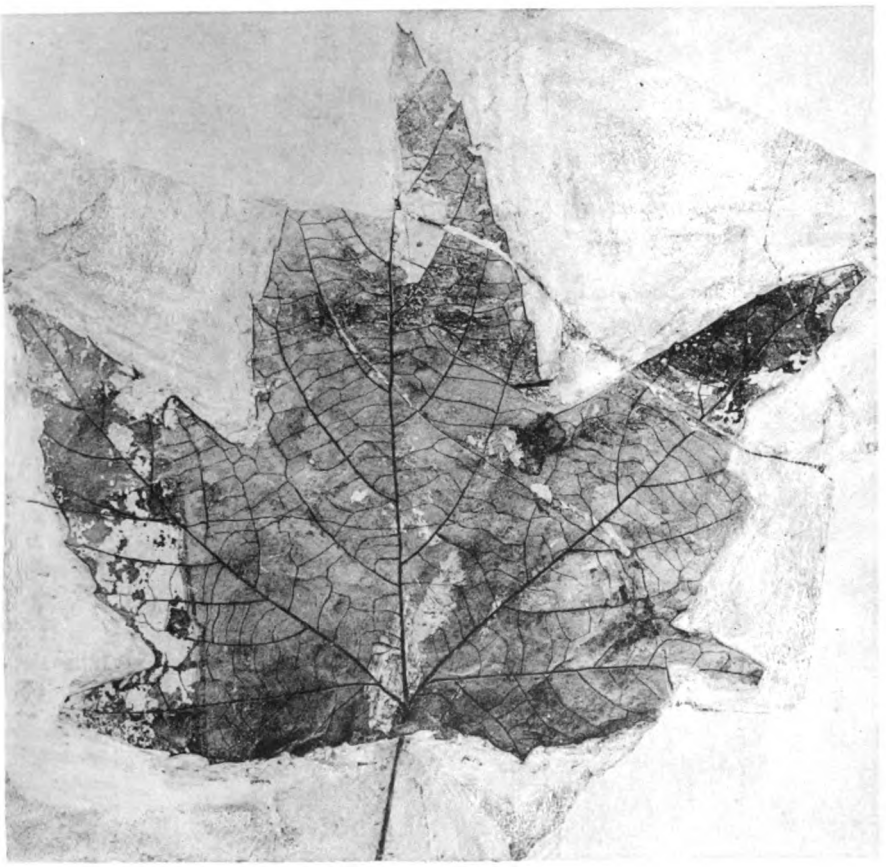

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PLATE 11

Remington Hill fossils

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Figs. 1–3. *Crataegus newberryi* Cockerell. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2422, 2420, 2421 49

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Fig. 5. *Platanus paucidentata* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2419 48

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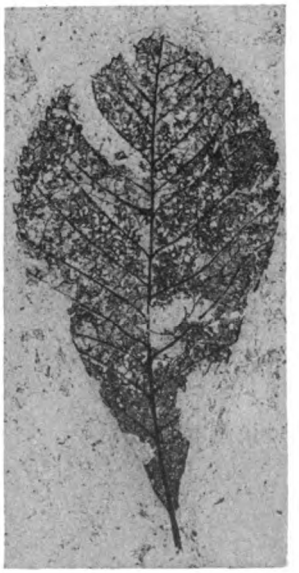

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PLATE 12

Remington Hill fossils

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Fig. 5. *Vitis bonseri* Berry. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2435 54

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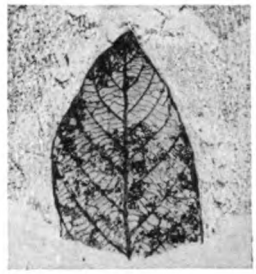

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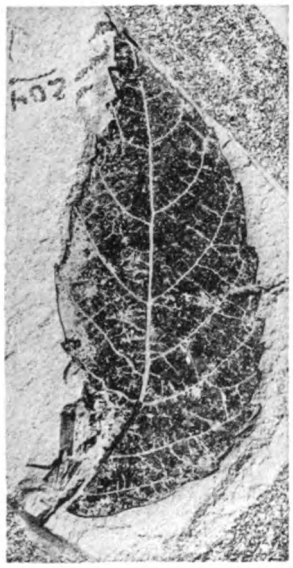

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3

The Table Mountain Flora

CARLTON CONDIT

Introduction

During the early days of gold mining in California, collections of fossil leaves were made from numerous localities where finer sediments were associated with the gold-bearing gravels. Lesquereux (1878*a*) studied several of these, including one from the andesitic sediments of Table Mountain, near Columbia, Tuolumne County, California. That exact locality is at present unknown, but extensive collections have been made in recent years from the same area at localities where the matrix is identical in all respects with that of the older collection.

After the first fossil leaves from Table Mountain were reported by Lesquereux, a few additional specimens were mentioned briefly by him (1883). Knowlton (1911) revised Lesquereux's work, rectifying several mistakes in localities and identifications. Chaney (1925*b*) discussed a florule from Buchanan Tunnel on Table Mountain in connection with the Mascall flora of eastern Oregon. In 1932 this locality was again mentioned in a catalogue of fossil-leaf localities (Chaney, 1932). Axelrod has discussed the Table Mountain flora in connection with the history of the Madro-Tertiary Flora (1938, 1939). Vertebrate material from Table Mountain was described by Merriam and Stock (1933), and has been discussed more recently by Stirton and Goeriz (1942).

The recent collections include most of the species described by Lesquereux, and in addition 14 species not previously recorded from the locality. With a total of 30 species, the Table Mountain flora is now sufficiently well known to provide reliable information regarding its age, and to indicate the climatic and topographic setting in this part of the Sierra Nevada during later Tertiary time. In addition, it increases our knowledge of the history of vegetation now living in California.

Acknowledgment for assistance in this study is gratefully made to Drs. H. L. Mason and Lincoln Constance, who have given much valuable advice, particularly in regard to the botanical aspects, and to Dr. B. L. Clark, who has considered the paleogeographic and stratigraphic problems. During the summer of 1937, R. L. Rist served as field assistant.

Geologic Occurrence

The striking topography of Table Mountain, and its proximity to the Mother Lode, early directed the attention of geologists to this region. Trask (1856) first described the distribution of its lava flow, and Whitney (1880), Ransome (1898, pp. 27–37; 1900, p. 6), and Turner (1894*b*, p. 466) have subsequently referred to

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it. Lesquereux (1878*a*) included a discussion of the Table Mountain flora in his report on the floras of the auriferous gravels. The only locality reference for this collection, which was made by C. D. Voy, is Table Mountain, Tuolumne County, California. There is no way of determining whether Voy's material came from Buchanan Tunnel, where our collections were made, or from one of the localities recently mentioned to the writer by Olaf P. Jenkins and Harry D. MacGinitie. They have noted poorly preserved leaf impressions in fine seams of clay in andesitic tuffs underlying the latite west of Jamestown and east of Tuttletown. In its species representation and excellence of preservation, Voy's material resembles our collections from Buchanan Tunnel. This is an old mine and was doubtless in operation when Voy was collecting fossil plants in the Sierra Nevada. It therefore seems probable that his specimens and ours are from the same locality. This assumption is supported by Turner's mention of the occurrence of *Persea pseudo-carolinensis* and *Ulmus californica,* determined by Knowlton, from Buchanan Tunnel, in "material . . . quite like the pipe clay of Tuolumne Table mountain" (1894*b*, p. 466).

Buchanan Tunnel, a drift mine now abandoned, is located on the northwest slope of Table Mountain, about 1½ miles west-southwest of Columbia, Tuolumne County, California, at an elevation of 2200 feet. It is in the NW. ¼ of Sec. 15, T. 2 N., R. 14 E., Mount Diablo Baseline and Meridian. This region is in the southern half of the southwest rectangle of the Big Trees Quadrangle, and lies near the divide on the west slope of the north fork of Stanislaus River. To the east, extensive placer mining operations have exposed the irregularly eroded basement of calcareous rock on several flats near Columbia. This limestone is referred to the Calaveras group, of Paleozoic age, and has been intruded by granodiorite of probable late Jurassic age. Resting on these older rocks are gravels and stream-sorted andesitic sediments which were included under the general term *auriferous gravels* by the earlier writers. In these channel deposits, capped by a latite flow, occur the gold which was sought by the miners of Buchanan Tunnel and the fossil plants which their digging uncovered. A general view of the locality and the surrounding vegetation is shown on plate 13.

Because of the complex history of channel cutting and deposition on the west slope of the Sierra Nevada, the age of the fossil-bearing beds is not readily determinable by standard stratigraphic methods. Earlier workers have determined their age as Pliocene (Lesquereux, 1878*a*, p. 54) and Miocene (Lindgren, 1911, pp. 55–57; Knowlton, 1911, pp. 57–64) largely on the basis of the plant fossils. Matthes (1930, pp. 27–29) has outlined the history of Tertiary uplifts in the northern Sierra Nevada, and has suggested approximate ages for the several sets of channel deposits, largely on physiographic evidence. He assigns the sediments below the lava cap of Table Mountain to the Miocene, and this assignment is corroborated by fossil determinations by Chaney and Stock. In a brief statement regarding the flora from Buchanan Tunnel, Chaney (1932, pp. 299–300) has assigned it an Upper Miocene age on the basis of the occurrence of many of its species in deposits of this age to the north. Considering the mammalian fossils in some detail, Merriam and Stock (1933) suggest the close

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relationship of two *Hipparion* teeth to *H. mohavense* and related types from the Ricardo deposits of the Mohave Desert, of Lower Pliocene age. They also indicate the possibility of an age as old as Upper Miocene. Louderback (1933) has shown that these horse teeth, from Number 2 Shaft of the Springfield Mining and Development Company, located 4200 feet southeast of the mouth of Buchanan Tunnel, occur in gravels immediately underlying the andesitic sediments in which our fossil leaves occur.

More recently Jenkins has made a comprehensive study of the placer deposits on the western slope of the Sierra Nevada, and in a thoughtful and highly suggestive paper (1935) has described the various criteria which are applicable to their age determination. We have benefited greatly by several discussions with him, and his helpful suggestions are gratefully acknowledged. His figures 21 and 31 show the complex stratigraphic relations of the sedimentary deposits, with figure 31 indicating the geologic cross section of Table Mountain in the immediate vicinity of the fossil locality. His conclusion that these leaf-bearing sediments are of Miocene age seems to have been based largely on Chaney's statement regarding the flora, mentioned above. With our larger collections, the age of the Table Mountain flora can be assigned to a position transitional between the Miocene and Pliocene; further evidence of the age of the flora is included in a later part of this chapter.

In their discussion of the Mokelumne area some 25 miles to the north of Buchanan Tunnel, Piper and coauthors (1939, p. 70) express the opinion that the leaf-bearing beds at the latter locality are equivalent to the lower part of the Mehrten formation. The correlation is largely lithologic, since there are no determinable fossils at the type locality. They indicate a probable Upper Miocene age for the Mehrten formation, and state that it may be in part Lower Pliocene.

Turning to the section exposed at and near Buchanan Tunnel, the hill which it penetrates is made up of some 50 to 75 feet of silt and tuff overlain by approximately 100 feet of andesitic cobble beds, coarse sand, and a 10- or 15-foot capping of coarse, angular andesitic agglomerate, a section corresponding closely to the type section of the Mehrten formation. An accurate section of the hill could not be determined, because of the thick soil and vegetation cover. The section exposed at the tunnel mouth is shown in the table on the following page. Although it is now impossible to enter the tunnel more than a few feet, information obtained from a former employee of the mine indicates that similar sediments extend downward for another 20 feet to thin gravels lying directly on bedrock at the channel bottom. An excellent description of this section is included in Louderback's paper, cited above.

All characteristics of these sediments suggest deposition by a stream flowing at low grade. Except for the basal gold-bearing gravels, the grains are usually very fine, the bedding is thin and regular, and cross-bedding is rare. Beds frequently lens abruptly, sometimes with a vertical contact, suggesting small-scale channeling. Many of the beds strongly resemble material deposited today along streams as a result of diurnal variation of flow: a layer of material of visible

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Section at Buchanan Tunnel	*Thickness in feet*
12. Soil	2–3
11. Finely bedded clay and silt	2
10. Medium-bedded dark-gray clay and silt	1
9. Finely bedded clay with thin sandy layers, individual layers ⅛ to ¼ inch thick	0.3
8. Light-gray massive siliceous tuff	0.3
7. Dark brownish-gray, poorly consolidated sand	1.5
6. Well bedded gray clay and sand	5
5. Unconsolidated, well bedded gray sand, bedding slightly contorted	1–1.5
4. Finely banded clay and silt, with small pockets and lenses of sand	0.6
3. Light-gray fine-grained tuffaceous sand, faintly bedded	2–3
2. Finely bedded light-gray silt and clay, with abundant leaf impressions	1
1. Massive gray flinty tuff	4
Total	21.0–23.5

grains ⅛ to ¼ inch thick is succeeded by a thin layer of the finest clay particles. This succession recurs many times. Invertebrate trails are common, and occasional tetrapod trackways[1] were observed. Contacts between beds of different grain size may be sharp or gradational. Several prospect holes are distributed along the strike for a distance of 100 feet, and in no two of these does the section correspond in more than a general way. According to other observers, the channel in this area is wide, the walls are at low angles, tributaries enter at the same level as the main channel, and the sediments indicate that there were many interlacing small channels.

Little direct evidence as to the altitude of the site of deposition of the Table Mountain flora is available. Matthes' investigations (1930, pp. 32–33) at Yosemite Valley, 40 miles southeast of Buchanan Tunnel and at an elevation about twice as great, are suggestive. He has correlated the sediments at Buchanan Tunnel with the Yosemite upland or "broad-valley state" of the region about Yosemite Valley. The elevation of the floor of this valley was calculated to have been only about 800 feet above sea level, with the high peaks such as Mount Lyell rising no more than 4000 feet above sea level. The topography was mature, with broad valleys and low rounded hills rising only a few hundred feet above them. This region was drained by the Tertiary equivalent of the Merced River, and it is only reasonable to suppose that the Tertiary Stanislaus was essentially similar to it. It seems probable that the elevation of Buchanan Tunnel was somewhat less than 800 feet, and probably about 500 feet above sea level, at the time when the plant-bearing sediments were deposited. Although no traces of the former topography remain except in the bottoms of the channel, it was doubtless similar to that of the Yosemite region, though more subdued. If

[1] Frank E. Peabody, who has studied these trackways, regards them as having been made by salamandroids similar to species living in California today.

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that was the case, the highest hills and ridges may have been no more than 1000 feet high, with rounded, gently sloping profiles. As will be mentioned in the section on composition of the flora, the assemblage of fossil plants represents communities that lived both along the stream and on the slopes of adjacent hills. This mingling in itself suggests that there was no high relief in the Columbia region at the time when the plant-bearing sediments were deposited.

Composition and Physical Indications

The Table Mountain flora is represented by more than 1000 specimens, among which 30 species have been recognized in 28 genera, 19 families, and 12 orders. One form has not been specifically named and 2 others are of uncertain position. Nine species are known only from this flora, of which 6 are here described for the first time.

Systematic List of Species

Spermatophyta
- Gymnospermae
  - Coniferales
    - Pinaceae
      - Pinus pretuberculata Axelrod
- Angiospermae
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Salix californica Lesquereux
    - Juglandales
      - Juglandaceae
        - Carya typhinoides (Lesquereux) new combination
    - Fagales
      - Fagaceae
        - Quercus bockéei Dorf
        - Quercus convexa Lesquereux
        - Quercus dispersa (Lesquereux) Axelrod
    - Urticales
      - Ulmaceae
        - Celtis kansana Chaney and Elias
        - Ulmus californica Lesquereux
    - Ranales
      - Berberidaceae
        - Mahonia prelanceolata new species
      - Magnoliaceae
        - Magnolia californica Lesquereux
      - Lauraceae
        - Persea coalingensis (Dorf) Axelrod
        - Umbellularia salicifolia (Lesquereux) Axelrod
    - Rosales
      - Saxifragaceae
        - Philadelphus nevadensis new species

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Platanaceae
Platanus dissecta Lesquereux
Rosaceae
Cercocarpus antiquus Lesquereux
Crataegus newberryi Cockerell
Leguminosae
Cercis buchananensis new species
Gleditschia sp.
Robinia californica Axelrod
Sapindales
Anacardiaceae
Rhus mensae (Lesquereux) Cockerell
Aquifoliaceae
Ilex opacoides new species
Aceraceae
Acer bolanderi Lesquereux
Rhamnales
Rhamnaceae
Berchemia multinervis (Al. Braun) Heer
Umbellales
Cornaceae
Cornus ovalis Lesquereux
Nyssa elaenoides (Lesquereux) new combination
Ericales
Ericaceae
Arbutus matthesii Chaney
Rhododendron sierrae new species
Gentianales
Oleaceae
Forestiera buchananensis new species
Incertae sedis
Ficus microphylla Lesquereux
Xanthoxylum (Zanthoxylon) diversifolium Lesquereux

Table 7 shows the relative abundance of the Table Mountain species. *Quercus convexa* and *Carya typhinoides* make up 35 per cent of the total, and with *Ulmus californica, Cercocarpus antiquus, Arbutus matthesii, Acer bolanderi,* and *Magnolia californica* comprise 69 per cent of the flora.[2] All but one of these probably were trees, three of them with hard, durable leaves which could easily withstand decomposition for a considerable time. Although the hickory (*Carya*) is second in abundance, a truer estimate of its relative representation in the forest might be obtained by dividing the number of leaflets by 5 or 7. Ninety-three per cent of the specimens represent 14 species, of which all but 3 (*Cercocarpus antiquus, Rhododendron sierrae,* and *Mahonia prelanceolata*) may be regarded as trees. This is in marked contrast with the least common 16 species, which make up only 7 per cent of the collection; most of these appear to

[2] *Ficus microphylla* and *Xanthoxylum diversifolium* are not considered in this discussion, since their true relations are unknown.

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TABLE 7

RELATIVE ABUNDANCE OF SPECIES IN THE TABLE MOUNTAIN FLORA

Species	*Field count*	*Collection*	*Total specimens*	*Per cent*
Quercus convexa	109	79	188	18
Carya typhinoides	117	64	181	17
Ulmus californica	58	37	95	9
Cercocarpus antiquus	32	59	91	8
Arbutus matthesii	40	30	70	7
Ficus microphylla	35	28	63	6
Acer bolanderi	38	17	55	5
Magnolia californica	32	18	50	5
Cornus ovalis	29	17	46	4
Persea coalingensis	27	16	43	4
Platanus dissecta	9	29	38	4
Rhododendron sierrae	21	13	34	3
Mahonia prelanceolata	10	11	21	2
Umbellularia salicifolia	10	6	16	1
Quercus bockéei	9	6	15	1
Salix californica	5	8	13	1
Cercis buchananensis	6	6	12	1
Berchemia multinervis	5	6	11	1
Forestiera buchananensis	2	6	8	
Rhus mensae	4	4	8	2
Ilex opacoides	2	3	5	
Robinia californica	3	2	5	
Nyssa elaenoides	3	2	5	
Quercus dispersa	2	1	3	
Crataegus newberryi	1	1	2	
Philadelphus nevadensis	0	2	2	1
Celtis kansana	0	1	1	
Gleditschia sp.	0	1	1	
Pinus pretuberculata	0	1	1	
Xanthoxylum diversifolium	0	2	2	
Total	609	476	1085	100

represent shrubs except *Cercis buchananensis, Gleditschia* sp., *Nyssa elaenoides, Pinus pretuberculata, Quercus bockéei,* and *Robinia californica.*

The Table Mountain flora is divisible into four elements on the basis of its relationships to modern vegetation, as shown in table 8. The West American Element, as represented by members of the Border-redwood and Rocky Mountain Components, has 8 species. The Southwest American Element, made up of the Oak woodland and Chaparral Components, includes 10 species. The East American Element is represented by 12 plants, and the East Asian by 3. Modern equivalent species of the Border-redwood Component of the West American Element range rather widely in California. Their occurrence in the Sierra Nevada, south Coast Ranges, and adjacent southern California in close association with living representatives of the Oak woodland and Chaparral

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TABLE 8

ELEMENTS AND COMPONENTS OF THE TABLE MOUNTAIN FLORA

Fossil species	*Equivalent living species*
West American Element	
Border-redwood Component	
Arbutus matthesii	A. menziesii Pursh
*Cercis buchananensis	C. occidentalis Torrey
*Cornus ovalis	C. californica C. A. Mey
Philadelphus nevadensis	P. lewisii Pursh
Pinus pretuberculata	P. attenuata Lemmon
*Platanus dissecta	P. racemosa Nuttall
Umbellularia salicifolia	U. californica Nuttall
Rocky Mountain Component	
*Acer bolanderi	A. grandidentatum Nuttall
*Cornus ovalis	C. stolonifera Michaux
Southwest American Element	
Oak woodland Component	
Celtis kansana	C. reticulata Torrey
Forestiera buchananensis	F. neo-mexicana Gray
Mahonia prelanceolata	M. lanceolata Fedde
*Persea coalingensis	P. podadenia Blake
Quercus convexa	Q. engelmannii Greene
Robinia californica	R. neo-mexicana Gray
Salix californica	S. breweri Bebb
Chaparral Component	
Cercocarpus antiquus	C. betuloides Nuttall
Quercus dispersa	Q. dumosa Nuttall
Rhus mensae	R. laurina Nuttall
East American Element	
*Acer bolanderi	A. acuminata Small
Berchemia multinervis	B. scandens Trelease
Carya typhinoides	C. cordiformis C. Koch
*Cercis buchananensis	C. canadensis Linnaeus
*Cornus ovalis	C. alternifolia Linnaeus
Gleditschia sp.	G. aquatica Marshall
Ilex opacoides	I. opaca Aiton
Magnolia californica	M. grandiflora Linnaeus
Nyssa elaenoides	N. sylvatica Marshall
*Persea coalingensis	P. borbonia Sprengel
*Platanus dissecta	P. occidentalis Linnaeus
Ulmus californica	U. americana Linnaeus
East Asian Element	
Crataegus newberryi	C. pinnatifida Bunge
Quercus bockéei	Asiatic Fagaceae
Rhododendron sierrae	R. rockii Wilson

*Species occurring in more than one component.

Components of the Table Mountain flora is highly suggestive of conditions at the time of floral deposition. In the central Sierra Nevada, equivalents of the Border-redwood Component are found commonly in canyons and on cooler slopes in woodland and chaparral country below the yellow pine zone. Such

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species as *Pinus attenuata* and *Cercis occidentalis* occur regularly in more open situations, but *Arbutus menziesii, Cornus californica, Philadelphus lewisii,* and *Platanus racemosa* are typically moist-slope or canyon-bottom in their modern distribution. Throughout their range the drier sites and steeper slopes near at hand contain such equivalents of the Chaparral Component as *Cercocarpus betuloides* and *Quercus dumosa.* Numerous live oaks, including *Quercus douglasii* and *Q. wislizenii,* form savanna and woodland associations over the adjacent uplands, and contribute also to the border-redwood forest. *Celtis reticulata* has a relict occurrence in the southern Sierra Nevada in Kern Canyon, in the oak woodland and chaparral country. Also occurring in this more southerly region is *Forestiera neo-mexicana,* closely related to the Table Mountain *F. buchananensis. Forestiera* extends into the south Coast Ranges and occupies river valleys in oak woodland and chaparral country, with border-redwood vegetation on cooler slopes at no great distance.

All these modern equivalent species except *Philadelphus lewisii* range into southern California, where there are two other plants having close equivalents in the Table Mountain flora. *Quercus engelmannii,* which shows relationship to *Q. convexa,* one of the dominants of the Table Mountain flora, is common in the foothills of interior southern California from Pasadena southward into northern Baja California. It forms a savanna over the lowlands, with chaparral and border-redwood vegetation on adjacent slopes. The chaparral commonly includes *Cercocarpus betuloides, Quercus dumosa,* and *Rhus laurina,* although the latter is more nearly coastal over the greater part of its range. *Cornus, Platanus,* and *Arbutus* are common in canyons. The knob-cone pine, *Pinus attenuata,* occurs in southern California only on the middle flanks of the San Bernardino Mountains, where it is in the ecotone between the chaparral and yellow pine zones. The majority of these species, however, extend to lower levels in the canyons and contribute their leaves, seeds, and twigs to accumulating sediments along with those of the Engelmann oak. *Celtis* and *Forestiera* are found also in the woodland and chaparral country of interior southern California, but are relicts in this region; they are more common in the southwestern United States.

Three members of the Oak woodland Component, *Mahonia prelanceolata, Persea coalingensis,* and *Robinia californica,* have equivalent species in the southwestern United States and northern Mexico. *Robinia* is common in canyons in Arizona, ranging from the yellow pine forest, where it is associated with equivalents of the Rocky Mountain Component, to lower levels in the oak woodland and chaparral country. In the former area it lives with *Philadelphus* and *Cornus* along stream valleys. *Acer bolanderi* is another member of the Rocky Mountain Component finding a relative in this region: *A. grandidentatum* is scattered through canyons in the Transition forest and in the upper part of the woodland. There is also a madrone in this region, *Arbutus arizonica* Sargent, but its slender leaves are more like those of *A. idahoensis* (Knowlton) Brown than our Table Mountain specimens, which resemble *A. menziesii.* On the lower edge of this zone, and in habitats similar to the ecotone

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between the Upper Sonoran and Arid Transition zones in California, these species are found with equivalents of the Oak woodland and Chaparral Components. In the canyon bottoms there are *Celtis reticulata* and *Forestiera neomexicana,* as well as a sycamore, *Platanus wrightii* Watson, which is similar to *P. racemosa* of California. The chaparral of the adjacent slopes resembles that in California, and commonly includes *Cercocarpus betuloides* and *Quercus turbinella* Greene, which show relationship to the fossil *C. antiquus* and *Q. dispersa. Cercis occidentalis* also lives here, occupying a position in woodland and chaparral. One of the common Arizona oaks is *Quercus oblongifolia,* which is related to *Q. engelmannii* of California, and to the Table Mountain *Q. convexa.* It forms extensive savanna and woodland associations which are frequently interrupted by chaparral. Two members of the Oak woodland Component, *Mahonia prelanceolata* and *Persea coalingensis,* find equivalent species in the Sierra Madre Occidental several hundred miles farther south in Sonora and Sinaloa. Here *Mahonia lanceolata* and *Persea podadenia* Blake live in the pine-oak and woodland country together with a number of species that range northward into Arizona.

Representatives of the East American Element have their nearest equivalents in the hardwood deciduous forests of the eastern United States, with most of them centering between latitudes 30° and 35°. This latitudinal distribution compares closely with that of many of the living relatives of species of this element in the Neroly and Remington Hill floras. Throughout their range in the Appalachian region they are found in the lowlands as well as some distance up the slopes. Most of these species range westward to Oklahoma and Texas, where they occupy valleys and flood plains in regions surrounded by more xeric types of vegetation. These habitats are more suggestive of Table Mountain conditions than is the humid Appalachian area to the east, judging by the abundance of associated oak woodland and chaparral species. Though the modern equivalents of *Magnolia californica* and *Persea coalingensis* are restricted eastward, it may be noted that there are species of magnolia and avocado in semiarid areas of northern Mexico showing nearly equal relationship to the fossil species. Historically, they are regarded as relicts of the Caribbean Element which was dominant in central California in the Eocene (MacGinitie, 1941), and survived in more coastal situations into the late Tertiary. The Neroly flora, from a coastal situation to the west, includes *Magnolia californica, Persea pseudo-carolinensis,* and *Tetracera castaneaefolia* MacGinitie. Other species of the Caribbean Element have been recognized by Axelrod in the Miocene of coastal southern California (1939, pp. 68–69). These species together with the associated East American Element presumably lived near sites of deposition, much as their equivalents do today in the more arid parts of their distribution. This would account for their abundance in the Table Mountain flora, where half the specimens are included in them.

The East Asian Element, *Crataegus newberryi, Quercus bockéei,* and *Rhododendron sierrae,* finds its modern relationships in regions where the climate and vegetation are essentially similar to those of eastern North America. These

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species are relicts of an element that was more abundant in the western United States in Miocene time; it occurs regularly with the East American Element in the Columbia Plateau and adjacent areas. The East Asian Element evidently was not common in the Table Mountain area, since it is represented by only a few specimens.

On the basis of their relative abundance and the habits of their living equivalents, the regional distribution of the Table Mountain species may be reconstructed as follows: Along the stream courses and valley bottoms, perhaps extending into this region from the coastal plain to the west, were *Magnolia californica, Persea coalingensis,* and *Platanus dissecta.* Bordering these on the lower slopes of the valleys, and in the more protected places such as north-facing slopes, were such species as *Berchemia multinervis, Carya typhinoides, Cercis buchananensis, Cornus ovalis, Nyssa elaenoides, Philadelphus nevadensis, Quercus bockéei, Rhododendron sierrae,* and *Ulmus californica.* They probably represent a downward extension of a forest more prominently developed in somewhat more mesic sites. On drier slopes, apparently at no great distance from sites of deposition judging from their abundant occurrence, were *Cercocarpus antiquus* and *Quercus convexa.* With their associates, *Celtis kansana, Forestiera buchananensis, Pinus pretuberculata, Quercus dispersa,* and *Robinia californica,* they formed woodland and chaparral communities. In view of these relationships it would appear that the Table Mountain region represented an ecotone between (1) the Arcto-Tertiary Flora (West American, East American, East Asian Elements), which originated in the north earlier in the Tertiary, and (2) the Madro-Tertiary Flora (Southwest American Element), which had extended northward into central California from the Mexican plateau region by the end of the Miocene.

As in the case of all Tertiary floras of western North America, the representation of several elements in the Table Mountain flora makes necessary a careful weighing of divergent evidence before the climatic factors can be adequately interpreted. Equivalents of the Border-redwood, Oak woodland, and Chaparral Components now found in California live in a region where there are moderate winters and warm to hot summers. Rainfall is limited to the winter season, most of it falling in the months from November to April. Precipitation varies from as much as 40 inches near Placerville in the central Sierra Nevada, where equivalent species of these components live together, to 20 or 25 inches in interior southern California in similar situations. Some of the equivalent species, such as *Celtis reticulata* and *Forestiera neo-mexicana,* also extend into drier areas where rainfall is about 10 inches yearly, and others, such as *Arbutus menziesii* and *Umbellularia californica,* range northward into regions where rainfall exceeds 50 inches. The majority, however, are found together in regions where precipitation ranges from 25 to 30 inches.

Equivalents of the Table Mountain flora in the southwestern United States range from lower elevations near the desert well upward to the Transition forest, where they meet representatives of the Rocky Mountain Component. Rainfall in the lower part of the woodland and chaparral country averages about

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12 to 15 inches yearly, whereas in areas where the woodland and chaparral are associated with the Transition forest, the rainfall commonly exceeds 20 inches. From the composition of the Table Mountain flora it may readily be determined that conditions in the ecotone between the Transition forest and woodland and chaparral country offer the nearest approximation to Table Mountain climate. Precipitation in the Southwest differs largely from that in California in having a biseasonal distribution, as summer showers and winter rains. Summers are hotter here than in any of the other areas where the flora finds equivalent vegetation, with average monthly means approximately 80° F., and extremes considerably higher.

Living equivalent species of the East American Element attain optimum development in the central Appalachian area, where annual rainfall ranges from 40 to 50 inches yearly, but, as indicated above, comparisons may better be made with conditions on the drier borders of their distribution at the west. This conclusion is suggested also by the fact that the leaves of *Ulmus americana* in the western parts of its distribution have the small size of *U. californica* of the Table Mountain flora. Most of the equivalents of the East American Element range westward into Kansas, Oklahoma, and Texas into areas where rainfall is as low as 25 to 30 inches, with some of the more hardy members of this group, notably *Cercis canadensis* and *Ulmus americana,* extending into regions with a precipitation as low as 17 inches. Rainfall in this western area tends toward biseasonal distribution, in contrast with that farther east, where it is distributed rather evenly throughout the year. Summers are warm to hot, and winters are mild, although freezing conditions are not uncommon. Climatic data are not readily available for members of the East Asian Element, but their equivalent species are believed to have requirements generally similar to those of the East American Element.

Mild winters were a regular feature of Table Mountain climate, but a diversity of summer temperatures is indicated, especially by the members of the Southwest American Element. This may result from the fact that the latter occupied more exposed habitats on drier slopes, whereas members of the other elements were more closely restricted to stream courses, valley bottoms, and moister slopes.

From this discussion it may be concluded that the Table Mountain area had an annual rainfall of from 25 to 30 inches. Whereas the East American, East Asian, and Southwest American Elements suggest that rain fell during the summer months, equivalents of the Border-redwood, Oak woodland, and Chaparral Components now limited to California indicate summers almost wholly without rain. A more critical examination of the distribution of modern relatives of these components, however, shows that they are not necessarily indicative of dry summer climate. All of them extend into regions where summer rains are frequent, or are represented in such areas by closely similar species. Paleobotanical data strongly suggest that they have become adapted to conditions of summer drought only since late Tertiary time (Axelrod, 1939, pp. 58–60). The weight of the evidence strongly implies that appreciable and ef-

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fective amounts of summer precipitation marked the climate of the Table Mountain flora.

The conditions postulated differ considerably from those at Table Mountain today. The station of the U. S. Weather Bureau nearest to the fossil locality is at Sonora, Tuolumne County, about 5 miles southeast of Table Mountain and 200 feet lower, and should record approximately the same climate. It is to be noted, however, that climate in this area varies widely with topography. Sonora lies in a relatively narrow canyon with hills several hundred feet higher both to the east and to the west. Climatic data for this station, therefore, must be modified somewhat in order to obtain a true picture of general climatic conditions on this part of the Sierra Nevada slope. Rainfall generally would be greater, and summer temperatures lower, than is indicated by the data set forth in table 9. Rainfall is moderate, falling almost wholly in the winter and early spring months. The hottest part of the year coincides with the driest season, which places a premium on a plant's ability to obtain moisture from ground water. Winter temperatures are moderate, with long or intense freezing spells rare. The frostless season usually lasts considerably more than 200 days, between April and November.

TABLE 9

CLIMATIC DATA FOR SONORA, CALIFORNIA

Month	Monthly and annual av. temperature (°F.)	Monthly and annual max. temperature (°F.)	Monthly and annual min. temperature (°F.)	Monthly and annual av. precipitation (in.)
January	43.8	52.8	34.8	6.85
February	47.0	56.6	37.4	5.92
March	50.8	62.2	39.4	6.39
April	56.3	69.6	43.0	2.31
May	60.5	75.3	45.7	1.72
June	69.3	84.7	53.9	0.27
July	75.8	91.7	60.0	0.02
August	73.6	89.7	57.6	0.04
September	67.8	81.6	53.9	0.56
October	58.6	71.1	46.1	1.90
November	50.4	61.7	39.2	3.36
December	45.4	55.2	35.7	5.68
Annual	58.3	71.0	45.6	35.02 (total)

The estimated 25- to 30-inch rainfall for Table Mountain time is 5 to 10 inches lower than that at Sonora today. This is a result of uplift of the region fully 1500 feet following the deposition of the flora. The trend in yearly rainfall in this region since Table Mountain time may be gauged from precipitation today at elevations comparable with those at which the flora lived. Annual rainfall in the Sierran foothills at 500 feet is estimated to average about 18 to 20 inches, as gauged from a 14-inch total at Oakdale, which lies 25 miles to the west and

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200 feet above sea level. Comparison with that postulated for Table Mountain time leads to the conclusion that precipitation has decreased approximately 10 inches. Summer moisture has been markedly lowered, since practically no rain falls in the region from June through September, and summer temperatures are considerably higher than those of Table Mountain time.

The physical conditions characterizing the Table Mountain area may be summarized as follows:

1. The flora is preserved in fluviatile, andesitic sediments deposited in a broad river valley in a region of moderate relief, 500 feet above sea level on the coastward slope of the central Sierra Nevada.

2. Members of the Border-redwood and Rocky Mountain Components of the West American Element, together with those of the East American and East Asian Elements, occupied stream banks and cooler slopes. Trees and shrubs of the Oak woodland and Chaparral Components of the Southwest American Element lived on exposed bordering slopes.

3. Table Mountain climate was characterized by 25 to 30 inches of annual rainfall, distributed as winter rains and summer showers. Temperatures in winter and summer were more moderate than those prevailing in the region today.

Age of the Flora

Twenty-one of the 30 Table Mountain species have been recognized in other fossil floras in western North America, as shown in table 10. The age of the Table Mountain flora will first be discussed in terms of these occurrences. Five Table Mountain species are known in Oligocene and Lower Miocene floras of California, Oregon, and Washington. Of these, *Arbutus matthesii, Berchemia multinervis, Cornus ovalis,* and *Platanus dissecta* occur elsewhere in floras as young as Pliocene. Only *Crataegus newberryi,* of the East Asian Element, has not previously been recorded in Pliocene floras of western North America. *Ulmus speciosa* of these older floras differs from *U. californica* in its larger leaves. *Ulmus californica* is known only from later Tertiary floras, apparently having been derived from a *speciosa* type of elm later in the Tertiary in response to increased aridity.

Eleven Table Mountain species have been recorded in the Middle and Upper Miocene floras of the western United States. Four of these are represented in the Miocene floras of the Columbia Plateau and northern Great Basin. *Arbutus matthesii, Cornus ovalis, Platanus dissecta,* and *Umbellularia salicifolia* extend into the Pliocene, and all except *Umbellularia salicifolia* also range down into the Lower Miocene. Two related species in these floras are *Crataegus imparilis* Knowlton of the Mascall, which may not be different from the Table Mountain species, and the larger-leafed *Ulmus speciosa* discussed above.

Eight Table Mountain species occur in the early Middle Miocene Tehachapi flora of southern California (Axelrod, 1939). All of them except *Philadelphus nevadensis* and *Cercocarpus antiquus* are known also in the Pliocene of California, and *Philadelphus* might be expected there on the basis of its survival

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in scarcely modified form in the Sierra Nevada. Most of these plants are members of the Southwest American Element, which appears to have reached the latitude of central California during the late Miocene and early Pliocene. Their occurrence as an important part of the Table Mountain flora lends considerable weight to a transitional Mio-Pliocene age assignment.

Seven Table Mountain species are represented in floras transitional in age between Miocene and Pliocene. The small number of species in these floras is due to the fact that only a few transitional Mio-Pliocene floras are now recog-

TABLE 10

DISTRIBUTION OF TABLE MOUNTAIN SPECIES IN OTHER FOSSIL FLORAS

SPECIES (Total, 21)	OLIGOCENE AND LOWER MIOCENE			MIDDLE AND UPPER MIOCENE					TRANSITIONAL			PLIOCENE				
	Weaverville	Bridge Creek	Eagle Creek	Tehachapi	Latah	Succor Creek	Payette	Mascall	Remington Hill	Neroly	Lower Idaho	Ellensburg	Dalles	Mulholland	Mount Eden	Other California Pliocene
Acer bolanderi	...	...	...	...	...	...	...	...	...	...	...	o	...	x	...	....
Arbutus matthesii	...	x	...	...	x	...	...	x	x	...	...	...	...	x	...	....
Berchemia multinervis	x	...	...	...	...	...	...	...	x	x	...	...	...	x	...	....
Celtis kansana	...	...	...	x	...	...	...	...	...	...	...	x	...	x	...	x
Cercis buchananensis	...	...	...	...	...	...	...	...	...	...	...	x	x	...	...	....
Cercocarpus antiquus	...	...	...	x	...	...	...	...	...	...	...	...	...	...	...	....
Cornus ovalis	...	x	...	...	x	x	...	...	...	...	...	...	...	x	...	....
Crataegus newberryi	...	x	...	...	...	...	...	o	x	...	?	...	...	...	...	....
Magnolia californica	...	...	...	...	...	...	...	...	...	x	...	...	...	...	...	....
Mahonia prelanceolata	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	x
Nyssa elaenoides	...	...	...	...	...	...	...	...	...	...	...	...	...	x	...	....
Persea coalingensis	...	...	...	x	...	...	...	...	o	o	...	...	...	...	x	x
Philadelphus nevadensis	...	...	...	x	o	...	...	...	...	...	...	...	...	...	...	....
Pinus pretuberculata	...	...	...	...	...	...	...	...	...	...	...	...	...	...	x	....
Platanus dissecta	x	o	...	...	x	x	x	x	...	x	x	x	x	...	...	x
Quercus bockéei	...	...	...	...	...	...	...	...	...	...	...	...	...	x	...	x
Quercus convexa	...	...	...	x	...	...	...	...	...	...	...	...	...	...	...	x
Quercus dispersa	...	...	...	x	...	...	...	...	...	...	...	...	...	...	x	x
Robinia californica	...	...	...	x	...	...	...	...	...	...	...	...	...	...	...	x
Ulmus californica	...	o	o	...	o	...	...	o	x	...	x	x	x	...	...	x
Umbellularia salicifolia	...	...	...	x	x	...	...	x	x	x	...	...	...	x	...	x
Identical species	2	3	0	8	4	2	1	3	5	4	2	4	3	8	3	10
Related species	0	2	1	0	2	0	0	2	1	1	0	1	0	0	0	0
Identical species in epoch		5				11				7				17		
Related species in epoch		1				2				1				0		

x = identical species; o = related species.

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nized, and all of them have small numbers of species as compared with those of the Miocene. *Arbutus matthesii* and *Platanus dissecta* in these transitional Mio-Pliocene floras are wide-ranging species having no close stratigraphic significance. The elm is similar to the Table Mountain species, and differs consistently from the larger-leafed *Ulmus speciosa* of the Miocene. Four species are common to the Table Mountain and Neroly floras; in addition, the avocado, *Persea coalingensis,* is represented by a related if not identical species (*P. pseudo-carolinensis*). There are several important differences between the Table Mountain and Neroly floras. Such Table Mountain genera as *Acer, Carya, Cornus, Gleditschia,* and *Ulmus* might be expected in the Neroly if the floras are of the same age, but they are not known there. Similarly, the Neroly has *Alnus, Betula, Chionanthus, Populus,* and *Taxodium,* which are absent from the Table Mountain flora. These differences, however, are due to environment, not to age. The Neroly flora was laid down essentially at sea level on the borders of a marine embayment 90 miles west of Table Mountain, and is characterized by mesic lowland flood-plain species. The Table Mountain flora, from an altitude of some 500 feet on the flanks of the Sierra Nevada, is made up of upland plants, many of which suggest a drier habitat. The Remington Hill flora, which grew to the north at an elevation of approximately 1500 feet above that of the Table Mountain flora, contains a more mesic group of plants, including such species as *Chamaecyparis gracilis, Liquidambar pachyphyllum, Sequoia langsdorfii,* and *Smilax diforma,* than is known from Table Mountain. Members of the Oak woodland and Chaparral Components are subordinate as compared with their representation at Table Mountain, much as they are today at higher levels where rainfall is greater. The differences among these three fossil floras appear to be of the same order as that in the modern vegetation over a corresponding range of altitude in California today.

Sixteen Table Mountain species have been recorded in Pliocene floras of California, with 4 of these, *Mahonia prelanceolata, Nyssa elaenoides, Pinus pretuberculata,* and *Quercus bockéei,* known only from the Pliocene. Five of the species, *Arbutus matthesii, Berchemia multinervis, Cornus ovalis, Platanus dissecta,* and *Umbellularia salicifolia,* occur in older and more northern floras. Most of the remainder seem largely referable to the Southwest American Element that invaded the lower western flanks of the central Sierra Nevada at about the end of the Miocene (Axelrod, 1938, 1939). Their large quantitative representation in the Table Mountain flora indicates a somewhat drier climate than is typical of the Upper Miocene, and thus suggests that the flora is somewhat younger.

In summary, table 10 shows that 5 Table Mountain species are known in older Miocene floras to the north, and 8 in the Miocene to the south, with a total of 11 in older Miocene floras on the Pacific coast; all but 2 of these are known in post-Miocene floras. Sixteen have been recorded from the Pliocene of California and Oregon, of which 5 are restricted to this epoch. With the exception of *Cercocarpus antiquus,* every species in the table has been recorded elsewhere in beds of Upper Miocene or Pliocene age, or has a closely similar species

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there. This distribution indicates an age close to the Mio-Pliocene boundary.

It has become increasingly apparent in recent years that the occurrence of species in other floras is not the only major basis for age determination. A study of the changes in distribution and composition of fossil floras in response to a climatic trend toward aridity during the Tertiary provides a more critical basis for age evaluation. Two floras which constitute excellent examples of this method are found in the High Plains (Chaney and Elias, 1936) and the Tehachapi (Axelrod, 1939). Ample evidence from the paleobotanical record of western North America indicates that there was a general southward migration of temperate vegetation during the Tertiary. This explains the relationship between the Table Mountain flora and the Upper Miocene floras of the northern Great Basin and Columbia Plateau. In view of the difference in latitude, we conclude that the Table Mountain flora is probably somewhat younger than Upper Miocene. Associated with this southward migration there appears to have been coastward movement, largely as a result of reduced or restricted seasonal precipitation. This phenomenon is regarded as responsible for the similarity between the Table Mountain and Mulholland floras. The Coast Ranges were rising during the Pliocene, and the climate at the interior was gradually becoming more continental. This would gradually restrict humid forest trees and shrubs of the Sierra Nevada westward to the Coast Ranges. Thus the similarity of the Table Mountain to the Mulholland and other Pliocene floras in the Coast Ranges of California suggests that the Table Mountain is somewhat older. Since the Mulholland is regarded as early Middle Pliocene, the Table Mountain can scarcely be younger than earliest Pliocene on the basis of its large East American Element. As was mentioned previously, the presence of a large representation of the Southwest American Element in the flora also lends weight to a Mio-Pliocene age assignment.

Such an age reference agrees closely with the interpretation of the vertebrate fossils from the Columbia district. Merriam and Stock (1933), in discussing the *Hipparion* from Springfield Shaft, come to the conclusion that it is essentially transitional Mio-Pliocene. According to R. A. Stirton (oral communication, August 1940), the Columbia *Hipparion* is the most primitive known from North America, and is similar to forms from Ingram Creek and Two Mile Bar (Stirton and Goeriz, 1942). In the type section of the Orinda formation, which is regarded as contemporaneous with the Neroly formation, there is a cannon bone similar to those from Ingram Creek and Two Mile Bar. The vertebrate evidence, therefore, suggests that the Table Mountain beds are of the same age as the Neroly flora.

Summary

The Table Mountain flora, comprising 30 species, occurs in andesitic sediments equivalent to the lower Mehrten formation, deposited in the lower foothills of the central Sierra Nevada. The West American and East American Elements are well represented, together with prominent members of the Southwest American Element. Varied topography is indicated, with a climate in-

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volving rainfall distributed in both winter and summer. Subsequent reduction in precipitation, with a summer drought and increased temperature extremes, seems related to the rising Coast Ranges at the west, and to fundamental climatic changes during later Cenozoic time. Reference of the Table Mountain flora to a transitional Mio-Pliocene age is based on geologic relations and the evidence of the plants and associated vertebrates.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA

Class GYMNOSPERMAE

Family PINACEAE

Pinus pretuberculata Axelrod

(Plate 14, figure 1)

Pinus pretuberculata Axelrod, Carnegie Inst. Wash. Pub. 476, III, p. 166, pl. 3, figs. 3, 4, 1937.

In 1937 Mr. E. E. Northrup, of Columbia, California, contributed a mold of the proximal part of a pine cone obtained in the andesitic mudflow of Table Mountain. It was found near Tuttletown, Tuolumne County, about 4 miles southwest of Columbia, and probably not more than 2 or 3 miles from Buchanan Tunnel. The mudflow is part of the same material that overlies the fossil-bearing sediments at Buchanan Tunnel; thus the cone is probably of the same age as the other fossil plants discussed in this paper.

The mold beautifully preserves the superficial characters of the original cone, which was evidently closely related to the modern *Pinus attenuata* Lemmon. This species is distributed from southern Oregon to northern Baja California at elevations of from 1000 to more than 5000 feet. It is one of the pioneers in burned or cut-over areas, and most commonly inhabits dry slopes and poor soil areas.

The illustration shows a cast made from the original mold by the personnel of Work Projects Administration O. P. 65-1-08-62, Unit A-1.

Occurrence. Near Tuttletown, Calif., loc. unknown.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2720.

Class ANGIOSPERMAE

Subclass DICOTYLEDONES

Family SALICACEAE

Salix californica Lesquereux

Salix californica Lesquereux (in part), Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 10, pl. 1, figs. 19, 21 (not figs. 18, 20, which are *Robinia californica* Axelrod), 1878.

The types of *Salix californica* represent two different species. The short, broad oval leaves illustrated by Lesquereux (figs. 18, 20) represent *Robinia,* and are placed in synonymy under *R. californica* Axelrod. The two slender leaves (figs. 19, 21) are retained as *Salix californica* Lesquereux. Since they are poorly preserved, and

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since no additional leaves were found at Buchanan Tunnel, it is difficult to evaluate the modern affinities of *S. californica*. *Salix breweri* Bebb has leaves resembling the fossils. In California it is most common on the dry inner side of the Coast Ranges, at elevations of about 1000 or 1200 feet in the north and as high as 3700 feet in the south. Typically it is distributed throughout the Upper Sonoran life zone.

Occurrence. Table Mountain, loc. unknown.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1878, 1879.

Family JUGLANDACEAE

Carya typhinoides (Lesquereux) new combination

(Plate 14, figures 7, 8; plate 16, figure 5; plate 19, figure 3)

Rhus typhinoides Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 29, pl. 9, figs. 1–6, 1878.

Quercus olafseni Heer. Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 245, pl. 54, fig. 3, 1883.

Lesquereux suggested that *Rhus typhinoides* was related to *R. typhina* Linnaeus (*R. hirta* Sudworth), although he pointed out several differences between the living species and the fossils. Comparison with herbarium material suggests that these differences are more important than Lesquereux believed. Leaflets of *R. typhina* differ consistently from the fossils in having a truncate base, prominent teeth, and secondaries whose angle of departure from the midrib is the same from near the tip to near the base. Leaflets of *Carya cordiformis* C. Koch (*C. amara* Nuttall), on the other hand, do not show these differences, and certain specimens in the University of California Herbarium (sheets 379138, 141866, 215438) are almost exactly like the fossils. In those fossils which have more than one leaflet still attached to the rachis, the terminal leaflet has a long-cuneate base and the lateral leaflets have narrow-truncate or cordate bases. This character does not appear in *Rhus typhina,* whose terminal leaflets are commonly much broader than the laterals and sometimes have teeth so large that they might be considered lobes. No impression of such a leaflet is present in the collections from this locality.

Leaflets of *Juglans californica* Watson are also similar to the fossils. Ecological arguments perhaps favor this genus, but only slightly more than they support *Carya*. The following morphological characters are common to *Carya cordiformis* and the fossils, but do not appear in *Juglans californica:* leaflets usually with curved sides and acuminate tips, rather than parallel sides and blunt tips; secondary veins bifurcating once or twice, with the branches leading into marginal teeth; tertiary veins prominently percurrent. It would seem, therefore, that these fossils should be assigned to *Carya* rather than to either *Rhus* or *Juglans*.

Carya cordiformis ranges from southern Canada to Alabama and Georgia, and westward to Minnesota and eastern Texas, being most abundant in Iowa, Nebraska, and Kansas. It occurs farther north than any other species of the genus, and is rarely found on the lower coastal plain along the Atlantic or Gulf shore. It inhabits moist, well drained soil either along bottoms or on higher rolling ground.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1889, 1890, 1891, 1892, 1893, 1894, 1913; plesiotypes, nos. 2723, 2724, 2725, 2773; nos. 2726, 2727, 2728, 2729.

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Family FAGACEAE

Quercus bockéei Dorf

(Plate 15, figure 2)

Quercus bockéei Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 84–86, pl. 9, figs. 1–3, 1930.
Fagus antipofii Heer. Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 3, pl. 2, fig. 13, 1878.

Leaves assigned by Lesquereux to *Fagus antipofii* were evidently rare in the Buchanan Tunnel forests, since only one specimen is present in his collections, and only one fragmentary specimen has been collected more recently. The material available appears to be allied to certain species of *Quercus* rather than to *Fagus*. Leaves which Dorf calls *Quercus bockéei* seem identical with the Table Mountain material. Dorf's discussion of *Q. bockéei* goes fully into the difficulty of separating *Quercus, Fagus,* and *Castanea,* and gives evidence for referring Lesquereux's specimens to *Quercus.*

In his discussion of the Mulholland flora, Axelrod (p. 134 below) suggests that *Q. bockéei* is more closely related to Asiatic forms than to any American oak.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1914; no. 2730.

Quercus convexa Lesquereux

(Plate 14, figures 2, 3, 5, 6)

Quercus convexa Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 4, pl. 1, figs. 13–17, 1878.
Quercus elaenoides Lesquereux (in part), *ibid.,* p. 4, pl. 1, figs. 10–12 (not fig. 9, which is *Nyssa elaenoides* (Lesquereux) Condit).
Myrtus oregonensis Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 254, pl. 58, fig. 10, 1883.

Lesquereux apparently separated *Quercus convexa* and *Q. elaenoides* on the basis of the small size and thick texture of *Q. convexa.* Although he noted that both species were similar to the leaves of the modern *Q. virens* Aiton (*Q. virginiana* Miller), comparison of the fossils with herbarium material indicates that they have closer affinities with *Q. oblongifolia* Torrey and *Q. engelmannii* Greene of western North America. Both the fossil species are included in the range of leaf variation of any of these living species.

Myrtus oregonensis Lesquereux, from Corral Hollow, represents a slender leaf of *Quercus convexa.*

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1869, 1870, 1871, 1872, 1873, 1874; plesiotypes, nos. 2731, 2732, 2733, 2734.

Quercus dispersa (Lesquereux) Axelrod

Quercus dispersa (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 97–98, pl. 7, figs. 8, 9, 1939.
Rhus dispersa Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 32, pl. 1, fig. 23, 1878.

The leaf described as *Rhus dispersa* by Lesquereux resembles most closely the living *Quercus dumosa* Nuttall. Some of the small oak leaves in subsequent collections

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may also be related to this species. On the other hand, they may be only variants of *Q. convexa*. *Quercus dumosa* is a "scrub oak" common in the chaparral of southern and central California, occurring at elevations usually of 1000 to 5000 feet.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1901.

Family ULMACEAE

Celtis kansana Chaney and Elias

(Plate 14, figure 4)

Celtis kansana Chaney and Elias, Carnegie Inst. Wash. Pub. 476, I, pp. 38–39, pl. 5, figs. 1–5, 1936.

Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 100–101, pl. 8, fig. 7, 1939.

One well preserved leaf clearly represents this species. Although it is somewhat smaller than the types, the details of margin and venation are closely similar both to the Kansas fossils and to the living *Celtis reticulata* Torrey, to which the fossil species is thought to be related. *Celtis reticulata* occurs on hillsides and in canyon bottoms, from western Texas and Oklahoma to southern California.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2737.

Ulmus californica Lesquereux

(Plate 18, figure 6)

Ulmus californica Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. 7*a*, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 46, pl. 8, fig. 4, 1944 (see synonymy).

Lesquereux recognized two species of *Ulmus* from Table Mountain, separating *U. affinis* from *U. californica* on the basis of the former's long petiole and close secondary veins, as well as on the presence of minor differences in the margin. He considered *U. californica* to be related to the living *U. alata* Michaux, but made no statement as to the modern relative of *U. affinis*. A comparison of all the fossils with elm leaves in the University of California Herbarium shows a much closer resemblance to *U. americana* Linnaeus. Inasmuch as the standard procedure in present-day Tertiary paleobotany is to distinguish fossil species only when they are clearly separable on the basis of modern species, Lesquereux's two species are here treated as one.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1917, 2735; no. 2736.

Family BERBERIDACEAE

Mahonia prelanceolata new species

(Plate 15, figure 3)

Description. Leaflets narrowly lanceolate, broadest a short distance above the base, strongly asymmetrical at the base, becoming symmetrical above; length preserved 4.1 to 8.6 cm. (5.5 and 10.0 cm. estimated), width 1.5 to 2.0 cm.; no petiole, the leaflets being sessile; numerous secondaries, diverging from the midrib at from 30° to 45°, looping well within the margin, with branches forming small loops nearer the margin; tertiaries forming a fine, angular mesh; margin spinose-serrate, the teeth

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widely separated and terminating the prominent tertiaries outside the looped secondaries; texture moderately thick.

Discussion. This species has been found only in the recent collections from Buchanan Tunnel. The fossils are almost exactly matched by leaflets of *Mahonia* (*Berberis*) *lanceolata* Fedde, a small tree or shrub growing in central Mexico at elevations of from 4500 to 5500 feet. It appears to be most common in canyons and washes where ground water is present during most of the year.

There is one fragment of a large leaf which may belong to *M. hollicki* (Dorf) Arnold (1936, p. 61). Only 4 cm. of the base is preserved. It is 2.5 cm. wide 2 cm. above the base, and in size and shape it is similar to *M. hollicki*. Its length cannot be estimated accurately; it may be short and broad, like *M. hollicki,* or long and slender, like *M. prelanceolata.*

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2738; nos. 2739, 2740, 2741.

Family MAGNOLIACEAE

Magnolia californica Lesquereux

(Plate 16, figure 4)

Magnolia californica Lesquereux (in part), Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 25, pl. 6, fig. 5 only, 1878.

Persea pseudo-carolinensis Lesquereux (in part), *ibid.,* p. 19, pl. 7, fig. 2 only.

Both the specimens that Lesquereux described as *Magnolia californica* were supposed to have come from Chalk Bluffs; only one (pl. 6, fig. 7), however, is actually from that locality, and is now considered by MacGinitie probably to be *Pongamia* (1941, pp. 132–133). The other (pl. 6, fig. 5) is definitely from Table Mountain, and Knowlton later recognized a similarity between this leaf and the leaf from Table Mountain which Lesquereux named *Persea pseudo-carolinensis* and illustrated on plate 7, figure 2. Knowlton (1911, p. 59) referred both these Table Mountain leaves to the genus *Persea,* but in the opinion of the writer they are *Magnolia* rather than *Persea.* It should be added that the specimen of *Persea pseudo-carolinensis* which Lesquereux described and illustrated on plate 7, figure 1 is definitely from the Chalk Bluffs flora and is considered by MacGinitie (1941, p. 119) to be a valid species. These fossils show relationship both to *M. grandiflora* Linnaeus and to *P. borbonia* Sprengel, but they more closely resemble *Magnolia,* as is shown by the following comparison: (1) *Persea* has always a much narrower leaf than *Magnolia;* (2) *Persea* usually has the lower secondaries pointing upward at much more acute angles than *Magnolia,* sometimes so much so that the leaves have a pli-nerved aspect; (3) the tertiary veins in *Persea* are usually much less pronounced than in *Magnolia,* so that there is a distinct difference in areolation, the veins being all of about equal size and extremely fine in *Persea,* whereas in *Magnolia* there is a very fine set of small nervilles within a coarser set of larger nervilles or tertiaries. Although these characters may not be applicable throughout all the species of both genera, they seem to hold for the two species here involved, at least on the basis of the material in the University of California Herbarium. They also serve to separate the fossils of these two genera collected from Buchanan Tunnel. This evidence indicates that the two specimens referred by Knowlton to *Persea,* and additional material in subsequent collections from the same beds, are probably referable to *Magnolia,* and are closely related to *M. grandiflora.*

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Magnolia grandiflora is a large evergreen tree found in moist, well drained soil from North Carolina through the Gulf States to Texas, and up the Mississippi Valley. It is most common on the borders of rivers and swamps, but occasionally occurs in the hills as well.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1803, 1804; plesiotype, no. 2742.

Family LAURACEAE

Persea coalingensis (Dorf) Axelrod

(Plate 16, figure 6)

Persea coalingensis (Dorf) Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 131–132, 1944 (see synonymy and discussion).

A number of avocado leaves in the Table Mountain flora may be referred to this common Pliocene species. They are more slender, as well as somewhat smaller, than those of *Persea pseudo-carolinensis* Lesquereux in the Neroly, Remington Hill, and Chalk Bluffs floras. *Persea coalingensis* shows a general relationship to the slender leaves of *P. borbonia* Sprengel of the southeastern United States, but is related also to the living *P. podadenia* Blake of the Sierra Madre Occidental in Sonora and Durango. This avocado lives in the pine-oak country together with another species, *Mahonia lanceolata* Fedde, which has a fossil representative in the Table Mountain flora.

Persea coalingensis may be represented in the Neroly flora from Corral Hollow by the slender leaf figured by Lesquereux as *Laurus princeps* Heer (Lesquereux, 1883, pl. 58, fig. 2). Unfortunately, there is now not sufficient material to make this correlation certain.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2743; no. 2745.

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939 (see synonymy).

There are a number of leaves of *Umbellularia salicifolia* in the Table Mountain flora, and they are indistinguishable from those of the living *U. californica* Nuttall. This species ranges from southern Oregon southward into northern Baja California. At the north it is associated with mesic coniferous forests; to the south it lives in canyons surrounded by xeric woodland and chaparral vegetation.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2721, 2722.

Family SAXIFRAGACEAE

Philadelphus nevadensis new species

(Plate 16, figure 2)

Philadelphus bendirei (Knowlton) Chaney. Axelrod, Carnegie Inst. Wash. Pub. 516, p. 104, 1939.

Philadelphus bendirei was first described as a species of *Cinnamomum* by Knowlton (1902, p. 59, pl. 10, fig. 4) on the basis of an incomplete specimen from the Bridge

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Creek locality in Oregon. With additional material from the type locality and from the Gray Ranch, Chaney (1927, pp. 118–120, pl. 17, figs. 1–5) placed the species in the genus *Philadelphus*. Brown (1940, pp. 350, 353) has recently placed the types in other genera, namely *Porana* and *Sassafras*. Oliver also recorded *P. bendirei* in the Blue Mountains flora (1934), but Brown has shown that it represents *Sassafras* (1937*a*). The specimen identified as *P. bendirei* by Axelrod in the Tehachapi flora, however, actually represents *Philadelphus*. It is, therefore, described as a new species, supplemented by the additional material in the Table Mountain flora.

Description. Leaves ovate, base bluntly cuneate, tip acute; 3 to 4 cm. long, 2 to 2.5 cm. wide; petiole 1 cm. long; midrib straight or slightly wavering, thick; pli-nerved, with or without a 4th and 5th vein outside the 3 major veins, the primaries arising a short distance above the base of the leaf; primaries and secondaries camptodrome, secondaries coarsely reticulate, often percurrent between the primaries, especially near the apex; tertiaries obscure, apparently reticulate; veinlets obscure; margin with few or several small or medium-sized remote teeth; texture medium.

Discussion. These fossils resemble in every way the smaller leaves found on the living *Philadelphus lewisii* Pursh, and may be regarded as representing a plant closely related to that species. *Philadelphus lewisii* has two varieties, one restricted to the coastal region from California to British Columbia, and the other extending inland over much the same latitudes. On the basis of the fossil leaves, it is difficult to decide whether one of these varieties is more closely related to the fossil species than the other. The most similar living species thus shows a wide range of tolerance, from the moist conditions of the redwood belt to the semiarid stream courses of central California.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2746; no. 2747.

Family PLATANACEAE

Platanus dissecta Lesquereux

(Plate 15, figures 1, 4)

Platanus dissecta Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 13, pl. 7, fig. 12; pl. 10, figs. 4, 5, 1878.

Aralia zaddachi ? Heer. Lesquereux, *ibid.*, p. 21, pl. 5, figs. 2, 3.

As Knowlton suggested (1911, p. 59), the fragments identified by Lesquereux as *Aralia zaddachi* are conspecific with *Platanus dissecta*. The similarities seen in the illustrations are augmented by an examination of the actual specimens.

Many authors have attempted, since *Platanus dissecta* was first described, to determine its status among the other fossil species of *Platanus* and its relationships to modern forms. The living *P. racemosa* Nuttall and *P. occidentalis* Linnaeus are the species with which this fossil has most often been connected. Lesquereux (1883, p. 249) regarded the fossil species as more nearly related to *P. racemosa* than to *P. occidentalis*, although he recognized its similarity to the eastern species in other contemporary studies. Dorf (1930, pp. 94–96) erected a new fossil species (*P. paucidentata*) which he considered to be equivalent to *P. racemosa*. LaMotte (1936, pp. 129–130) related *P. dissecta* to *P. racemosa*. He emphasized the similarity of the fossils to leaves of trees growing in more mesic habitats. In 1936, Dorf (1936, p. 117)

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interpreted this species as related to *P. occidentalis* on the basis of its strongly toothed stipules, although he likewise admitted the resemblance of the fossils to the California sycamore. Oliver (1934, p. 22) reached the same conclusion, on the same basis. Berry (1929, pp. 248–249) had previously stated that the leaves of *P. dissecta* found in the Latah flora were very similar to those of *P. racemosa,* and perhaps represented an ancestor of it. MacGinitie (1937, pp. 140–141), following Henry and Flood, used the depth of sinuses, as measured by the ratio of the square of the perimeter to the area, as a basis for associating *P. dissecta* with *P. orientalis* Linnaeus. In the Neroly flora the writer (1938, p. 262) considered *P. dissecta* to be closer to *P. occidentalis,* on the basis of morphology and ecology.

Considerable confusion thus exists as to the affinities of the fossil species *Platanus dissecta* with modern forms, as well as its relationship to *P. paucidentata.* The usual practice is to assign fossils with deep sinuses to *P. paucidentata* and those with shallow sinuses to *P. dissecta.* In the writer's material from Buchanan Tunnel there are no specimens comparable with the remarkably excellent leaves from which the species was described by Lesquereux. All the present specimens are too fragmentary to facilitate a solution of this perplexing problem. Chaney collected one specimen from the locality with relatively shallow sinuses, though not so shallow as is typical of leaves of *P. occidentalis.* The type specimens of *P. dissecta* resemble neither of the living species very closely, judging from the material in the University of California Herbarium. It is interesting to note that one sheet of *P. orientalis* (or *P. acerifolia*) in the herbarium has a leaf almost identical with Lesquereux's types. All the other leaves of this species, however, are quite dissimilar.

The confusion in regard to this species may be the result of attempts to construct precise relationships between Miocene and modern species, by correlating characters in the leaves of the two horizons. This can be done in some cases, but in many fossils of Pliocene age or older, it is to be expected that characters will suggest relationships with two or more modern species, especially if these are closely related or incompletely differentiated. This appears to be the case with *Platanus dissecta,* for these fossils have characters which seem to relate them to both *P. racemosa* and *P. occidentalis,* and show a close resemblance to certain leaves of *P. orientalis.* In view of these facts, and of the confusion about the status of many of the living species of *Platanus,* it seems impossible to state with certainty the relationships of the fossil and living forms.

The observable facts, however, support the conclusion that *Platanus* leaves with deep sinuses are characteristic of regions with abundant sunlight and low relative humidity, and that leaves with shallow sinuses are more common in regions with reduced sunlight during the growing season. This correlation is apparent not only in the differences between *P. occidentalis* and *P. racemosa,* but also in the variation among leaves of the latter species in different habitats, as has been previously pointed out by MacGinitie (1937). It is significant to note that the Table Mountain leaves represent neither extreme, but are intermediate in depth of sinus and probably indicate that the climate in which they developed was marked by moderate amounts of both heat and moisture. There is, at least, no evidence of extremes of either temperature or aridity.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1831, 1832, 1834, 1835; plesiotypes, nos. 2748, 2749; no. 1833.

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Family ROSACEAE

Cercocarpus antiquus Lesquereux

(Plate 16, figure 3)

Cercocarpus antiquus Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 37, pl. 10, figs. 6–11, 1878.

These leaves appear to be related to both the modern *Cercocarpus alnifolius* Rydberg and *C. betuloides* Nuttall, and less similar to other species of the genus. University of California Herbarium sheet 187678 of *C. alnifolius* has leaves that match closely many of the present fossils. Some of the fossils suggest leaves of *Crataegus,* but the presence of a single set of serrations with each point corresponding to a secondary vein excludes them from that genus.

Cercocarpus alnifolius is restricted to Santa Catalina and Santa Cruz islands off the coast of California, whereas the closely related *C. betuloides* is widely distributed throughout the foothills and lower mountain slopes from Baja California to Oregon and east to the Rockies. Both species are limited to drier regions at elevations of from 500 to 4000 feet, within the Upper Sonoran life zone.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2750; paratypes, nos. 1882, 1883, 1884, 1885, 1886, 1887; nos. 1888, 2751, 2752, 2753.

Crataegus newberryi Cockerell

(Plate 16, figure 1)

Crataegus newberryi Cockerell, Univ. Colo. Studies, vol. 5, p. 43, 1908.
Condit, Carnegie Inst. Wash. Pub. 553, p. 49, pl. 11, figs. 1–3, 1944 (see synonymy).

The single leaf referred to this species seems at first to be distinct from the leaves of any previously described *Crataegus.* It looks, however, much like Newberry's *C. flavescens,* which has been synonymized with *C. newberryi* by Cockerell. The Bridge Creek specimens of *C. newberryi* (Chaney, 1927, pp. 121–122) are of the more common *C. pinnatifida* shape, with pinnate venation and deep, serrulate lobes. The Table Mountain leaf is unlike these, being broad and short, and having a palmate appearance. When compared with modern leaves, however, it falls within the range of variation of *C. pinnatifida* Bunge of northern China, Korea, and eastern Siberia (see University of California Herbarium sheet 387680).

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2754.

Family LEGUMINOSAE

Cercis buchananensis new species

(Plate 17, figures 1, 3, 6)

Description. Leaves round, tip blunt, base deeply cordate; 6 cm. long, 7 cm. wide; petiole missing; midrib thin and straight, extending to the tip with very little reduc-

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tion in size; 3 thick primaries on each side, the basal pair somewhat smaller than the others, which are as thick as the midrib, branching dichotomously distally, with the branches also dichotomously dividing; secondary veins 3 from the midrib, opposite or subopposite, leaving midrib at angles of 20° to 30°, dichotomously branching distally as the primaries do; tertiary veins fine, irregularly percurrent, anastomosing with nervilles of almost equal thickness, which form fine quadrangular reticulation; margin entire, slightly thickened; texture medium.

Discussion. A preliminary examination of these fossils reveals at once their similarity to *Cercis.* Confusion has arisen regarding some fossil leaves originally referred to this genus (Berry, 1930*b*, p. 240) which were subsequently transferred by Brown (1937*a*, pp. 181–182) to the genus *Vitis.* The characters of the Buchanan Tunnel leaves, as described above, show that they are certainly not *Vitis,* but unquestionably belong to the genus *Cercis.*

These leaves differ from those of *Cercis* hitherto described in having rounded, blunt tips, and in their relatively large size. They are similar to leaves of the modern western redbud, *Cercis occidentalis* Torrey, but appear to be even closer to the eastern *C. canadensis* Linnaeus. Apparently these fossils were borne upon a plant combining the characters of the western and eastern redbuds.

Cercis canadensis is a tree which grows along streams and valley bottoms, from New Jersey and Pennsylvania to northern Florida, and from southern Ontario to the Sierra Madre in northeastern Mexico. *Cercis occidentalis* is a shrub or occasionally a small tree growing along streams in the Coast Ranges and the Sierra Nevada at altitudes of from 1000 to 4000 feet, and occurring southeastward into Texas. It is usually most abundant near the boundary of the Upper Sonoran and Transition zones.

Cercis buchananensis is also found in collections from The Dalles, Oregon (Chaney, chap. 11 below, pp. 319–320, pl. 51, fig. 1), and is very common at Ellensburg, Washington.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2755, 2756, 2757, 2757*a* (counterpart).

Gleditschia sp.

(Plate 17, figure 2)

One specimen in the collection from Buchanan Tunnel appears to represent a cast of half a seed of *Gleditschia.* It is about 1 cm. in diameter, about 5 mm. thick, rounded, with the attachment of the funiculus extended into a blunt point. The surface is marked by fine irregular striae or wrinkles extending obliquely across the seed. The fossil agrees in most external characters with *G. aquatica* Marshall, except that it is somewhat thicker than any specimens in the University of California Herbarium, and is perhaps smaller than the average seed of this species. The absence of leaves referable to *Gleditschia,* and the lowland habit of the modern species, also cast doubt on this identification. The writer has, however, seen no other seeds which approach the fossil so closely. The seeds of *Robinia,* a related genus represented in the flora by several leaflets, are considerably smaller and of different shape.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2758.

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Robinia californica Axelrod

(Plate 17, figures 4, 5)

Robinia californica Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 114–115, pl. 9, figs. 10–12, 1939.

Salix californica Lesquereux (in part), Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 10, pl. 1, figs. 18, 20 only, 1878.

Several leaflets from Buchanan Tunnel are conspecific with the material described by Axelrod from the Tehachapi flora. Some of them are smaller than the types, but are no smaller than many borne by the living equivalent, *Robinia neo-mexicana* Gray. *Robinia neo-mexicana* occurs throughout the southwestern United States and northern Mexico, occupying canyons and draws from near the desert to well up in the Transition zone.

Two of the types of *Salix californica* Lesquereux are leguminous, and cannot be differentiated from the leaflets of *Robinia;* the other two types are retained as *Salix californica* Lesquereux.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1875, 1877, 2759, 2760.

Family ANACARDIACEAE

Rhus mensae (Lesquereux) Cockerell

(Plate 20, figure 8)

Rhus mensae (Lesquereux) Cockerell, Amer. Jour. Sci., 4th ser., vol. 26, p. 543, 1908.

Rhus metopioides Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 31, pl. 8, figs. 12, 13, 1878.

As the original name implies, Lesquereux believed that these fossils were related to the modern *Rhus metopium* Linnaeus, which inhabits the West Indies and the southern tip of Florida. The ecological implications of such a relationship are not consonant with those furnished by the rest of the flora. The fossils are similar to *R. laurina* Nuttall, now living in southern coastal California and adjacent Mexico. This distribution is more nearly that which might be expected for a modern equivalent of a member of the Buchanan Tunnel flora.

Rhus prelaurina Axelrod (1937, pp. 180–181, pl. 6, fig. 12) is not here synonymized, because of insufficient material of both species.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1867, 1868; plesiotype, no. 2761; no. 2762.

Family AQUIFOLIACEAE

Ilex opacoides new species

(Plate 18, figures 3, 5)

Description. Leaves broadly oval; tip missing, probably acute; base acute; length preserved 5.6 cm. (6.5 or 7.0 cm. estimated), width about 4.0 cm.; petiole stout, 6 mm. long; midrib moderately stout, straight; 5 pairs of secondaries preserved, probably 6 or 7 pairs, alternate, leaving the midrib at angles of 50° to 75°, slightly wavering or going straight for more than two-thirds of the distance to the margin,

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then forming conspicuous loops; intersecondaries common, often nearly as strong as the secondaries, ending in the loops formed by the secondaries above and below; tertiaries forming an irregularly angular mesh inside the secondaries, and forming a series of prominent loops between the margin and the loops of the secondaries, with strong branches into the teeth and numerous finer branches to the margin between the teeth; margin thick, with 1 to 4 or 5 dentate, spiny teeth; texture subcoriaceous to coriaceous.

Discussion. The 2 specimens from Buchanan Tunnel representing this species are of considerable interest in the light of the suggested phylogeny of fossil hollies set forth in the discussion of *Ilex lomensis* of the Neroly flora (Condit, 1938, pp. 264–265). They somewhat resemble *I. sonomensis* Dorf, but on the basis of sheets in the University of California Herbarium are more similar to *I. opaca* Aiton than to *I. brandegeana* Loesener, to which *I. sonomensis* is most similar. Furthermore, the present fossils have characters, particularly of venation and margin, similar to those of *I. lomensis,* which is also considered close to *I. opaca. Ilex opacoides,* however, is like the living species and unlike *I. lomensis* in its smaller size, shorter, more ovate leaf, and smaller teeth. One of the most pronounced differences between *I. lomensis* and both *I. opacoides* and *I. sonomensis* is the much greater size of the Neroly species. This is probably the result of climatic changes in the later Tertiary, which reduced the amount of available water for plants on the west coast of North America. The Buchanan Tunnel specimens closely approach the size of *I. sonomensis,* and presumably were adapted to a restricted water supply. Since only 2 leaflets were observed in the collections, the species may be considered to have lived on hillsides at some distance from the stream channels, in areas where abundant water was not available throughout the year. *Ilex opaca* commonly grows in such situations today.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2763, 2764.

Family ACERACEAE

Acer bolanderi Lesquereux

(Plate 19, figures 5, 6)

Acer bolanderi Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 27, pl. 7, figs. 7–11, 1878.

In describing this species, Lesquereux stated that it most closely resembled *Acer tripartitum* Nuttall and *A. grandidentatum* Nuttall, both members of the Rocky Mountain flora. As judged from the material in the University of California Herbarium, the fossils bear little resemblance to *A. tripartitum* (now *A. glabrum* Torrey), but are quite similar to *A. grandidentatum.* A consistent difference from the latter species appears in the base, which is deeply cordate in the modern leaves, and almost square in the fossils. *Acer acuminata* Small, of the eastern United States, is also closely similar to the fossils. It has a more nearly square base, and in this character is a better match for the fossil leaves than *A. grandidentatum.* It is at present not feasible to select one of these species as the living equivalent of the fossil species to the exclusion of the other.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1825, 1826, 1827, 1828, 1829; plesiotypes, nos. 2765, 2766; nos. 2767, 2768.

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Family RHAMNACEAE

Berchemia multinervis (Al. Braun) Heer

(Plate 19, figures 1, 2)

Berchemia multinervis (Al. Braun) Heer, Flora tertiaria Helvetiae, vol. 3, p. 77, pl. 123, figs. 9–18, 1859.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 52–53, pl. 12, fig. 4, 1944 (see synonymy).

Specimens from Buchanan Tunnel are clearly identical with the fossils from the Neroly (Condit, 1938, p. 265) and the Remington Hill beds (chap. 2 above, p. 52). Although there are no clear physical criteria to distinguish *Berchemia* from *Karwinskia,* ecological arguments favor the reference of these specimens to the former genus. The American representative of the genus, *B. scandens* Trelease, is a vine widespread in the southeastern United States.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2769, 2770.

Family CORNACEAE

Cornus ovalis Lesquereux

(Plate 19, figure 4)

Cornus ovalis Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 23, pl. 6, figs. 1, 2, 1878.

More specimens of this species have appeared in later collections from Buchanan Tunnel. None of these is complete, yet sufficient material is preserved to verify the original identification and indicate the relation of the fossils to modern species. The fossil leaves are closely matched by leaves of *Cornus alternifolia* Linnaeus, a shrub or small tree distributed along stream borders and swamps from Nova Scotia and Minnesota south along the Appalachians, where it attains elevations of 4000 feet. There are certain western species, such as *C. californica* C. A. Mey, that show resemblance to the fossils. *Cornus californica* is a common valley shrub on the Pacific slopes of California and Oregon.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1902, 1903; plesiotype, no. 2771; no. 2778.

Nyssa elaenoides (Lesquereux) new combination

(Plate 18, figures 1, 4; plate 20, figure 7)

Quercus elaenoides Lesquereux (in part), Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 4, pl. 1, fig. 9 (not figs. 10–12, which are *Q. convexa*), 1878.

Arbutus matthesii Chaney (in part), Carnegie Inst. Wash. Pub. 346, IV, pp. 131–132, pl. 20, figs. 3, 4 only, 1927.

Description. Leaves ovoid, base cuneate, tip blunt; 5.0 to 7.0 cm. long (estimated), 2.8 to 4.4 cm. wide; petiole heavy, up to 1.7 cm. long; midrib wide below and thin above, but standing out prominently from the lamina; secondary veins subopposite near the base, alternate near the tip, about 6 mm. apart on the average, making angles of about 50° with the midrib, irregularly curved toward the tip, occasionally anastomosing, bifurcating near the margin, the branches forming loops by joining branches from adjacent secondaries; these branches give rise to a second set of loops,

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and these to a third very close to the margin; basal pair of secondaries arising nearly at juncture of lamina and petiole, leaving midrib with a reverse curve, and bearing small branches which form loops along the lower margin; intersecondaries leaving midrib at same angle as secondaries, very shortly bifurcating, with the branches joining the secondaries; tertiary veins forming coarse irregular network, nervilles a finer network between; margin entire, slightly revolute, texture medium.

Discussion. The leaves of *Nyssa elaenoides* are similar to those of the living *N. sylvatica* Marshall of the eastern United States. This species ranges from Maine westward to Michigan, Missouri, Oklahoma, and Texas, and southward into Florida, in habitats varying from mountain slopes to the borders of swamps. On the basis of its Table Mountain associates, it is considered to have occupied cooler and moister slopes bordering sites of deposition, in much the same way as the modern *N. sylvatica* occurs today in the western parts of its distribution.

Nyssa elaenoides is easily distinguishable from the larger-leafed *N. knowltoni* Berry, which is common in the Neroly flora of west-central California (Condit, 1938) and in several Miocene floras of the northern Great Basin and Columbia Plateau. *Nyssa knowltoni* seems more nearly related to *N. aquatica* Linnaeus than to *N. sylvatica* on the basis of its oval shape, its larger size, the occasional presence of large teeth, and the reflexed secondaries in the lower part of the blade.

The type of *Nyssa elaenoides* is based on one of the specimens of *Quercus elaenoides* Lesquereux, the others clearly being referable to *Q. convexa*. The 2 specimens of *Arbutus matthesii* cited above are from Table Mountain, and now seem more properly assignable to *Nyssa* than to *Arbutus*.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1922; plesiotypes, nos. 120, 121, 1923, 2744, 2776, 2777.

Family ERICACEAE

Arbutus matthesii Chaney

(Plate 20, figure 5)

Arbutus matthesii Chaney (in part), Carnegie Inst. Wash. Pub. 346, IV, pp. 131–132, pl. 20, figs. 1, 5 (not figs. 3, 4, which are *Nyssa elaenoides* (Lesquereux) Condit), 1927.

Chaney identified and described this species partly from material obtained at Buchanan Tunnel. Additional material in our collection fully corroborates the suggested relationship between *Arbutus matthesii* and the living *A. menziesii* Pursh of the Pacific states.

Two of the paratypes of *A. matthesii* are now considered to represent *Nyssa elaenoides* (Lesquereux) Condit, on the basis of their secondary venation and shape.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 119; plesiotype, no. 2772.

Rhododendron sierrae new species

(Plate 20, figure 6; plate 21)

Description. Leaf lanceolate, tip acuminate, base cuneate; 11.0 to 12.0 cm. long, 1.5 cm. wide at widest part, which is slightly above the middle of the leaf; petiole 2.0 to 3.0 cm. long, straight, thick; midrib thick, protruding from the under side of the lamina; secondary veins opposite to subopposite, numerous, about 5.0 to 7.0 mm.

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apart, leaving midrib at angles of 40° to 50°, running fairly straight or gently curved until main marginal curve begins, at which point they are reduced in size and become indistinguishable from tertiary veins; tertiaries of one size only, forming a closely spaced net of fine veins into which small subsecondaries extend for a few millimeters from the midrib; margin entire, revolute; texture thick.

Discussion. This genus is known in the fossil record of North America from only two occurrences, one in the early Tertiary of Alaska (Hollick, 1936, p. 160, pl. 99, fig. 4) and the other in the Trout Creek beds of eastern Oregon (MacGinitie, 1933, p. 64, pl. 7, fig. 4). The Trout Creek specimens were identified tentatively as *Rhododendron,* and no specific name was applied. MacGinitie noted its resemblance to modern species from southwestern China, but discussed its relationships no further.

The present specimen is very similar to the Trout Creek fossil, differing from it in being somewhat narrower and having apparently fewer secondaries. The University of California Herbarium contains several hundred sheets of various species of *Rhododendron* from the provinces of Szechwan and Yunnan in southwestern China and the eastern border of Tibet. Among these are several species which correspond closely to the present material, notably *R. floccigerum* Franchet, *R. poecilodermum* Balfour f. and Forrest, and especially *R. rockii* Wilson, as represented on sheet 381231. Most of the rhododendron leaves, even of the species cited, are broader than the fossils, although they approach closely the same proportions. All the other characters of the leaves in the majority of the species of this genus, however, are closely matched in the fossils. Both have entire revolute margins, the same arrangement of the secondaries, a thick midrib, and closely netted tertiaries. In addition, several of the fossils have a thick coating of carbonaceous matter which may represent the remains of the well developed covering of hair found on the lower surface of most rhododendron leaves. One of the fossils consists of a part of a branch with 11 fragments of alternately disposed leaves attached to it. It is quite possible that the Trout Creek and Buchanan Tunnel fossils represent the same species, even though the latter are consistently narrower than either the Trout Creek or the living material with which both have been compared.

The modern Chinese rhododendrons appear to be distributed at high altitudes, centering at 9000 to 12,000 feet in Yunnan, Szechwan, and adjacent Tibet. Unfortunately no information about the elevation at which *R. rockii* occurs is available, but presumably it, too, grows in the same places. One American species, *R. maximum* Linnaeus, from the Appalachian Mountains, approaches the fossils in general character. This species is distributed from Nova Scotia to North Carolina, commonly along streams at elevations up to 3000 feet. The fact that one of the fossils is a stem with 11 leaves attached indicates that it probably was not carried far before entombment, and hence grew close to the site of deposition.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2774, 2775.

Family OLEACEAE

Forestiera buchananensis new species

(Plate 20, figure 2)

Description. Leaf oblanceolate, base long acuminate, tip somewhat blunt; 4 cm. long, 7 mm. wide; petiole short or only partly preserved; midrib thick, protruding below lamina; secondary veins 7 pairs, opposite, leaving midrib at low angles,

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camptodrome close to margin, joining with secondaries above; tertiary veins scattered, forming coarse areolation; nervilles fine, forming dense quadrangular reticulation between tertiaries; margin entire, slightly revolute, with a small spine at tip; texture thick.

Discussion. This species is represented by one almost complete leaf and several fragments which are assigned to it doubtfully. It agrees with leaves of *Forestiera neo-mexicana* Gray, except that in the fossil the areolation of the nervilles is somewhat finer than in the modern leaves. It differs from *Forestiera* sp. Axelrod, reported from the Tehachapi flora (Axelrod, 1939, pp. 126–127, pl. 12, fig. 3*b*), in being considerably narrower and longer, as well as in its relationship to a different modern species.

Forestiera neo-mexicana occurs in southern California and eastward into Texas and Colorado, occupying valley flats or mountain canyons at elevations up to 5500 feet. In California it extends as far north as the Gabilan Range, only a little more than 1° south of the fossil locality.

Occurrence. Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2779.

INCERTAE SEDIS

Ficus microphylla Lesquereux

(Plate 20, figures 1, 3, 4)

Ficus microphylla Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 18, pl. 4, figs. 10, 11, 1878.

Ficus mensae Cockerell, Amer. Naturalist, vol. 44, p. 45, 1910.

With the addition of later collections to the 3 types designated by Lesquereux as *Ficus microphylla,* a total of 28 specimens is now at hand. Comparisons with herbarium material have not shown a close relationship to any modern genus. There is a general resemblance to *Philadelphus* in the size and shape of the leaves and in the pli-nerved base, but finer details do not agree. A Chinese *Cercis, C. liangkwangensis* Chun, is somewhat similar to the fossils, but the living leaves are thicker in texture, larger, and more asymmetrical at the base.

Since these leaves have been referred to *Ficus microphylla* by Lesquereux, and since no close modern relative has been found, they are placed in Incertae sedis under this name, although they are not considered to represent a fig.

Occurrence. Table Mountain, loc. unknown; Buchanan Tunnel, loc. P3715.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1810; plesiotypes, nos. 2780, 2781, 2785; nos. 1809, 2782, 2783, 2784.

Xanthoxylum (Zanthoxylon) diversifolium Lesquereux

(Plate 18, figure 2)

Zanthoxylon diversifolium Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 33, pl. 8, figs. 14, 15, 1878.

Fagara diversifolia (Lesquereux) Cockerell, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 98, 1908.

The 2 types of this species illustrated by Lesquereux are still the only representatives in the collections, since no new material referable to the species has been found. Knowlton (1911, p. 60) pointed out that the species was incorrectly attributed to

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Bowen's Claim, and is in reality from Table Mountain. Lesquereux suggested a relationship between the fossils and the living *Xanthoxylum triphyllum* of Brazil, an affinity which would seem to be ecologically incredible. In *Index Kewensis* there are listed 2 species bearing the name *Xanthoxylum triphyllum*. One, *X. triphyllum* G. Don, has been synonymized with *Evodia triphylla* DeCandolle, from the Malayan region; the other, *X. triphyllum* Wight, is synonymized with *Evodia roxburghiana* Bentham, from tropical Asia. It is possible that the material used by Lesquereux for comparison really came from Asia.

A satisfactory reference on the basis of the incomplete material available is manifestly impossible, but it is to be noted that there is some similarity between the fossil and leaf bases of *X. americanum* Miller, a species now living throughout much of the northern part of the eastern United States.

Occurrence. Table Mountain, loc. unknown.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1899, 1900.

Species Not Recognized as Members of the Flora

Several species in addition to the above forms have been listed by various investigators as occurring in the Table Mountain flora. These are:

Ilex prunifolia Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 27, pl. 9, fig. 7, 1878.

Rhus boweniana Lesquereux, *ibid.*, p. 29, pl. 9, figs. 9, 10.

Rhus myricaefolia Lesquereux. Chaney, Carnegie Inst. Wash. Pub. 349, II, p. 33, 1925.

Salix angusta Al. Braun. Chaney, *ibid.*

Salix varians Goeppert. Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 247, pl. 55, fig. 6, 1883.

This writer was unable to identify any of the material in his possession as belonging to these species. *Rhus boweniana,* as Lesquereux suggested, may not have been found at Table Mountain. *Salix varians* and *S. angusta* closely resemble the leaves of *Carya cordiformis* C. Koch, and may have been included in the equivalent fossil species. Specimens of the remaining 2 species have apparently been lost, and have not been found in more recent collections.

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PLATES 13—21

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FIG. 1. General view of Buchanan Tunnel, locality P3715. Digger pine, oak woodland, and chaparral now dominate the area, with occasional yellow pines.

FIG. 2. Buchanan Tunnel, locality P3715, showing the entrance to the tunnel

TABLE MOUNTAIN LOCALITY AND MODERN VEGETATION

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PLATE 14

TABLE MOUNTAIN FOSSILS

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FIG. 1. *Pinus pretuberculata* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2720 74

FIGS. 2, 3, 5, 6. *Quercus convexa* Lesquereux. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2731, 2732, 2733, 2734 76

FIG. 4. *Celtis kansana* Chaney and Elias. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2737 77

FIGS. 7, 8. *Carya typhinoides* (Lesquereux) Condit. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2723, 2724 75

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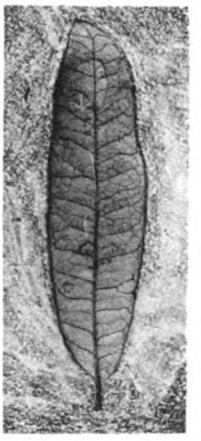

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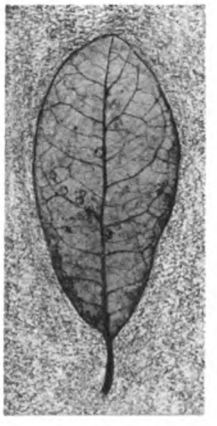

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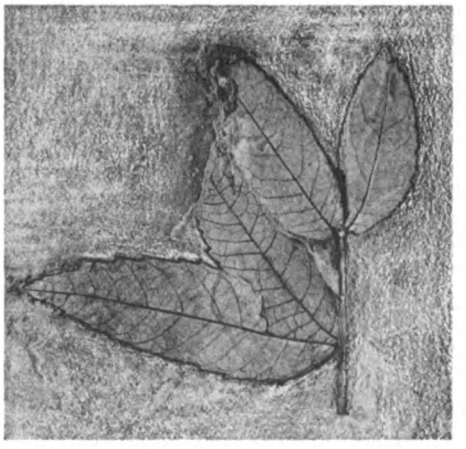

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PLATE 15

TABLE MOUNTAIN FOSSILS

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FIGS. 1, 4. *Platanus dissecta* Lesquereux. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2748, 2749 80

FIG. 2. *Quercus bockéei* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1914. This is a specimen figured by Lesquereux (1878*a*, pl. 2, fig. 13) as *Fagus antipofii* 76

FIG. 3. *Mahonia prelanceolata* Condit. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2738 77

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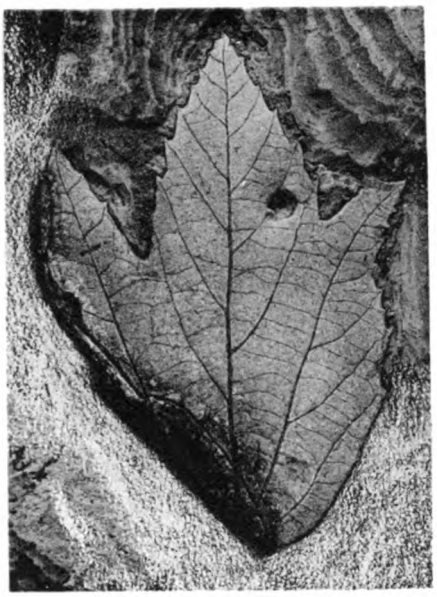

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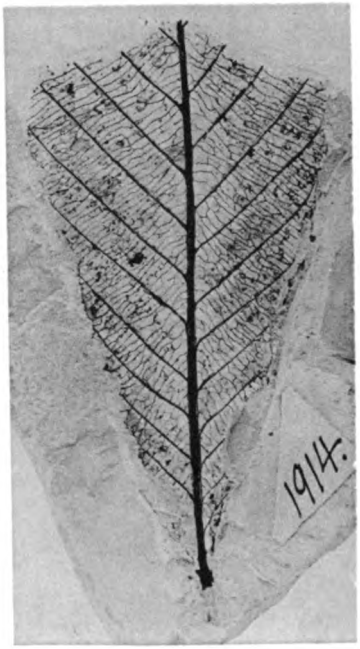

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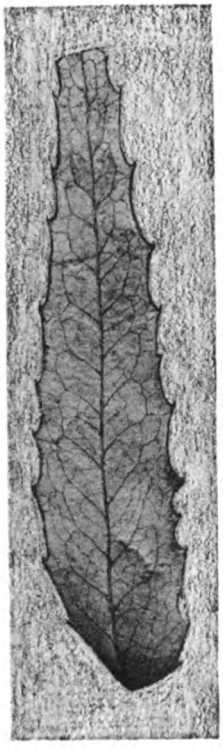

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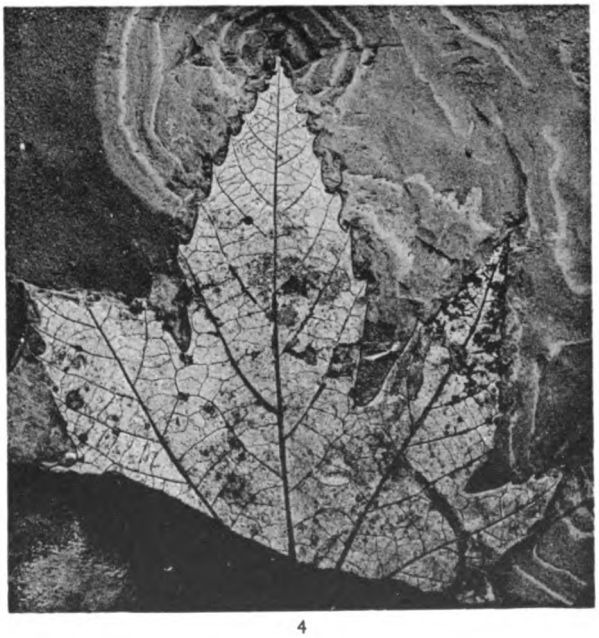

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PLATE 16

Table Mountain fossils

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Fig. 1. *Crataegus newberryi* Cockerell. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2754 82

Fig. 2. *Philadelphus nevadensis* Condit. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2746 79

Fig. 3. *Cercocarpus antiquus* Lesquereux. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2750 82

Fig. 4. *Magnolia californica* Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2742 78

Fig. 5. *Carya typhinoides* (Lesquereux) Condit. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2725 75

Fig. 6. *Persea coalingensis* (Dorf) Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2743 79

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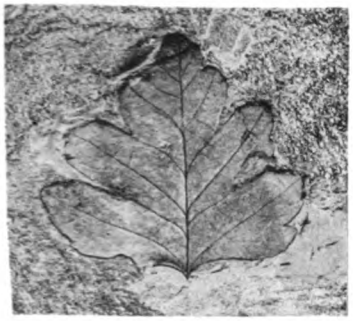

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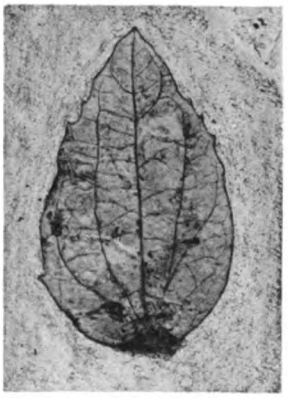

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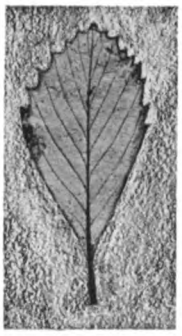

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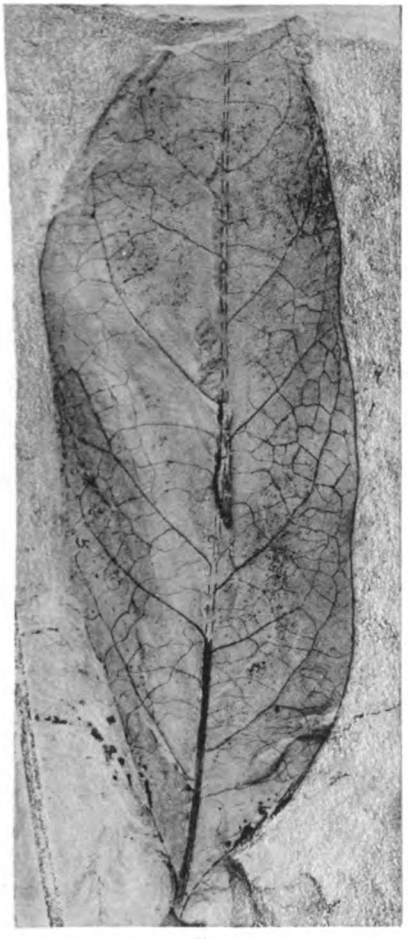

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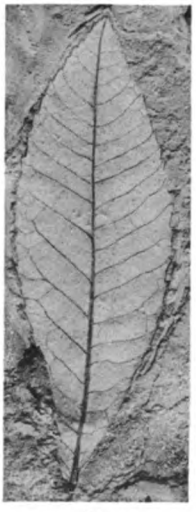

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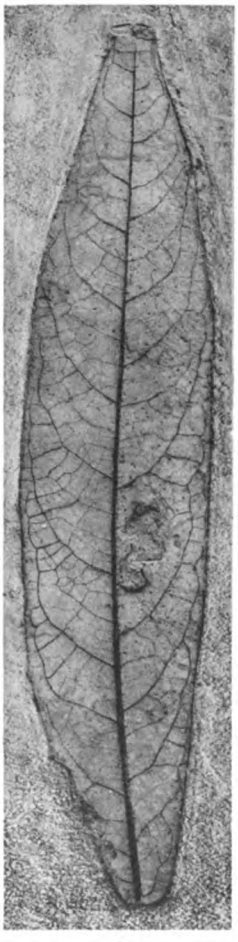

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PLATE 17

Table Mountain fossils

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Figs. 1, 3, 6. *Cercis buchananensis* Condit. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2755, 2757, 2756 82

Fig. 2. *Gleditschia* sp. U. C. Mus. Pal., Paleobot. Ser., no. 2758 . . . 83

Figs 4, 5. *Robinia californica* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2759, 2760 84

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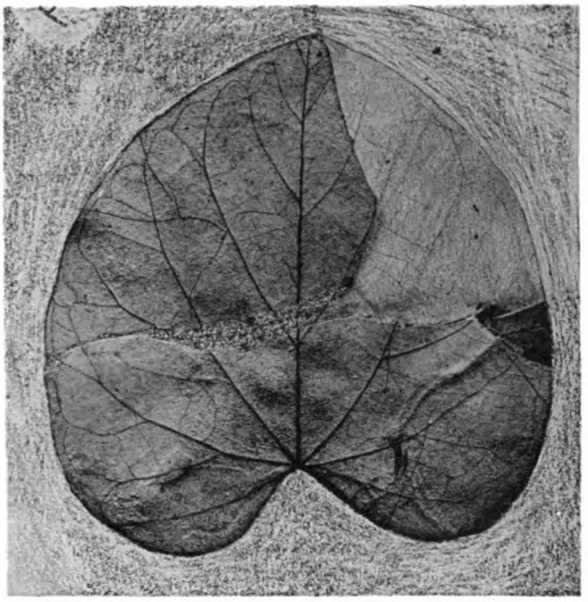

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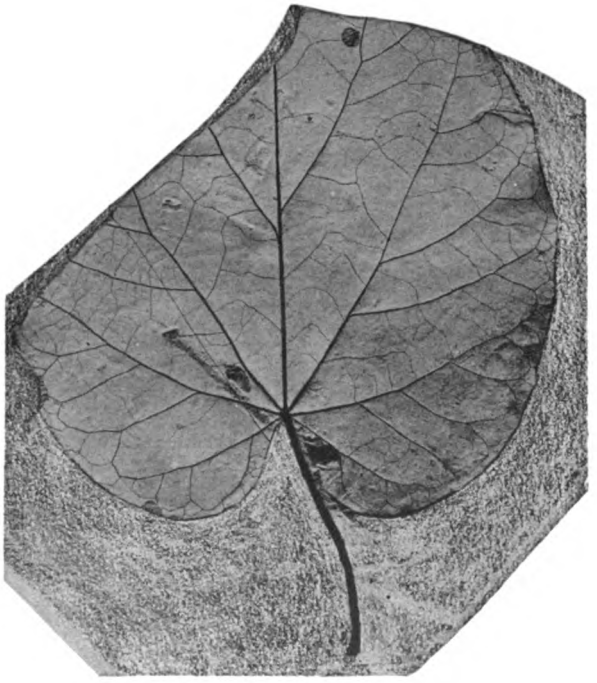

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PLATE 18

Table Mountain fossils

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Figs. 1, 4. *Nyssa elaenoides* (Lesquereux) Condit. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2776, 2744 86

Fig. 2. *Xanthoxylum* (*Zanthoxylon*) *diversifolium* Lesquereux. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 1900. This is a specimen figured by Lesquereux (1878*a*, pl. 8, fig. 15) 89

Figs. 3, 5. *Ilex opacoides* Condit. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2764, 2763 84

Fig. 6. *Ulmus californica* Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2735 77

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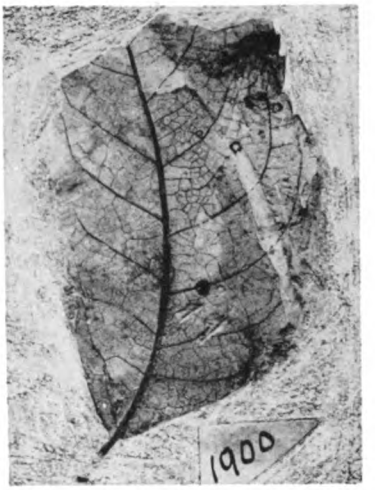

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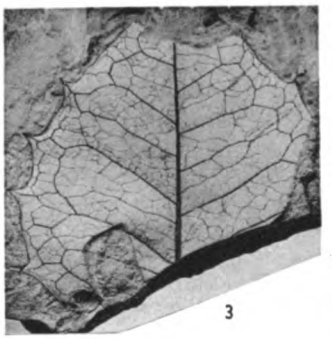

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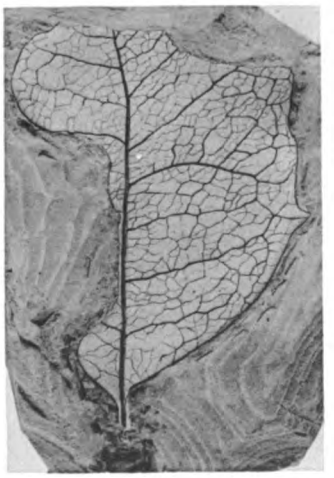

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PLATE 19

Table Mountain fossils

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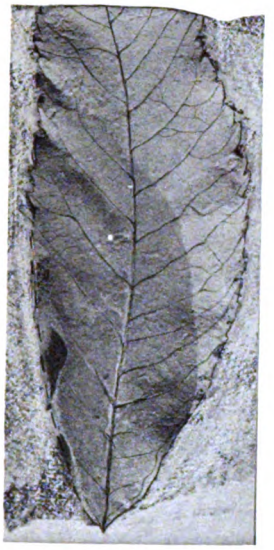

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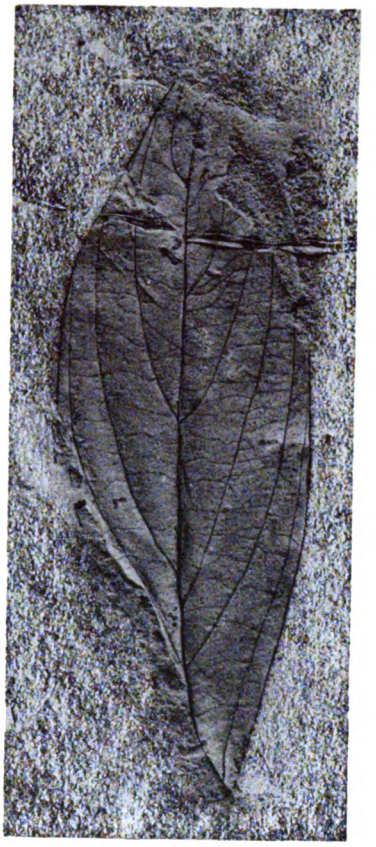

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Table Mountain fossils

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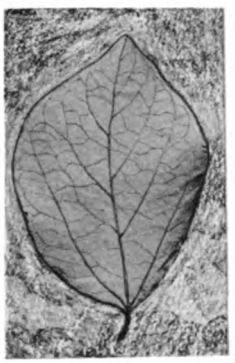

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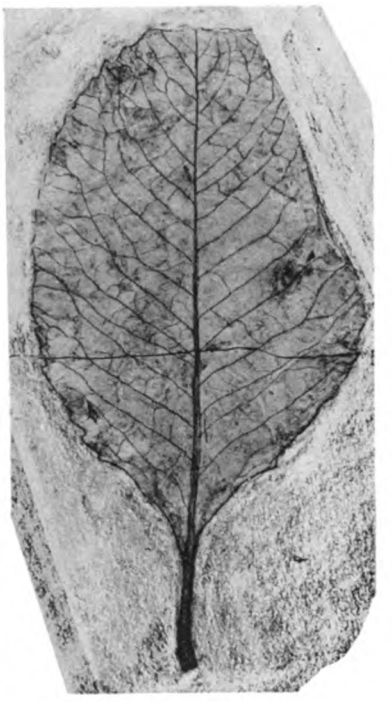

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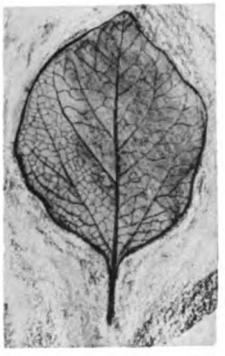

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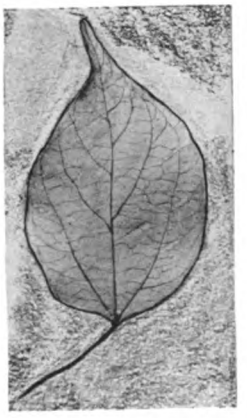

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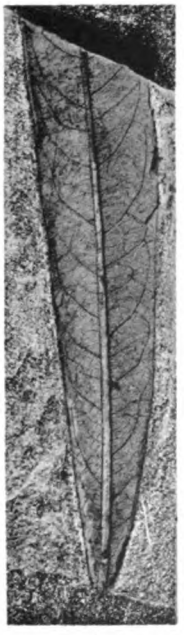

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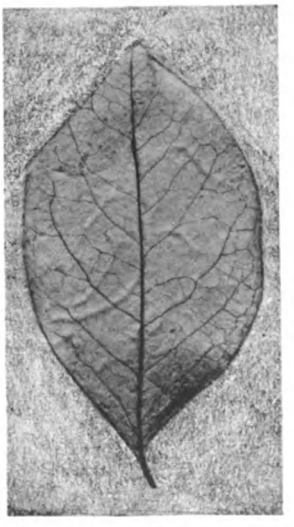

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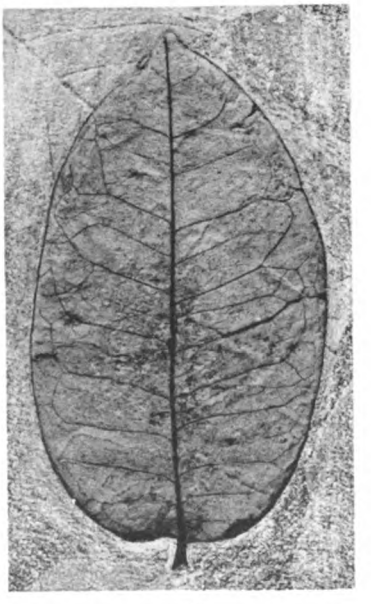

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TABLE MOUNTAIN FOSSILS

Rhododendron sierrae Condit. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 2775 . . . . . page 87

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4

The Black Hawk Ranch Flora

DANIEL I. AXELROD

Introduction

It is the purpose of this brief paper to record a small flora from the Black Hawk Ranch vertebrate quarry (Richey, 1938; Stirton, 1939*a*). Exposed on the southwestern flank of Mount Diablo directly east of San Francisco Bay, this quarry occurs near the base of the Green Valley formation as defined recently by Clark (1940). A small collection of fragmentary and poorly preserved fossil plants from this locality, constituting the Green Valley florule, was reported first by Condit in his discussion of the Neroly flora of this region (1938, pp. 248–250). In the course of further excavation for vertebrate material, Richey obtained plant material of a more diagnostic character, and this was generously turned over to the writer for study. Because the outstanding feature of this Lower Pliocene flora is its definitely Miocene aspect, it has an important bearing on the interpretation of Pliocene floras in the western United States.

Acknowledgment is made to Mr. R. C. Force, through whose cooperation collecting has been made possible on his Black Hawk Ranch.

Composition and Physical Indications

Leaf impressions are abundant in the gray clayey strata at the vertebrate quarry, but only the 8 species listed below have been determined. All these have been recorded elsewhere in the Miocene and Pliocene floras of the western United States.

Systematic List of Species

Spermatophyta
- Angiospermae
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Populus washoensis Brown
        - Salix hesperia (Knowlton) Condit
    - Fagales
      - Fagaceae
        - Quercus convexa Lesquereux
        - Quercus lakevillensis Dorf
    - Urticales
      - Ulmaceae
        - Ulmus californica Lesquereux

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Rosales
  Platanaceae
    Platanus dissecta Lesquereux
  Rosaceae
    Cercocarpus cuneatus Dorf
Sapindales
  Anacardiaceae
    Rhus moragensis Axelrod

On the basis of their relative abundance in the flora, as well as their climatic and floristic relationships, the species fall into two natural groups. They are listed below together with their nearest living equivalents:

Fossil species	*Nearest related modern equivalents*	*Nearest occurrence of equivalents*
Mesic flood plain		
Platanus dissecta	P. orientalis Linnaeus	Eastern Asia
	P. racemosa Nuttall	Near fossil locality
Populus washoensis	P. grandidentata Michaux	Eastern North America
Salix hesperia	S. lasiandra Bentham	Near fossil locality
Ulmus californica	U. americana Linnaeus	Eastern North America
Woodland-chaparral		
Cercocarpus cuneatus	C. betuloides Nuttall	Near fossil locality
Quercus convexa	Q. engelmannii Greene	Southern California
Quercus lakevillensis	Q. agrifolia Née	Near fossil locality
Rhus moragensis	R. ovata Watson	Southern California

Members of the flood-plain assemblage clearly dominate the flora, accounting for 195 of the 200 specimens examined. All the woodland-chaparral species are represented by single specimens except the live oak, *Quercus lakevillensis,* which has two; and it must be noted also that all show signs of transport from more distant areas. Judging by the thick and coriaceous leaves produced by their modern representatives, woodland-chaparral species would be expected to have been preserved in abundance had they lived near the immediate site of deposition.

By considering these groups from the standpoint of their relationship to fossil and modern plants, it is possible to approximate the physical conditions existing in the region during Black Hawk Ranch time. The abundant flood-plain group is dominated by the sycamore, *Platanus dissecta.* The relationships of the three Miocene and Pliocene species of *Platanus, P. aceroides, P. dissecta,* and *P. paucidentata,* to one another and to modern equivalent species have not been satisfactorily established. Our leaves have deeper lobes than are typical of *P. aceroides,* and are therefore referred to *P. dissecta,* which is the most widely distributed Miocene species in the western United States. Whereas the modern affinities of *P. aceroides* and *P. paucidentata* seem to be with *P. occidentalis* and *P. racemosa* respectively, *P. dissecta* shows relationship to *P. orientalis* and *P. racemosa.* It must be emphasized, however, that resemblance between *P.*

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dissecta and *P. racemosa* is found only with specimens of *P. racemosa* from the more mesic and coastal parts of its range; even here it is uncommon to find the deep scalloped teeth that characterize the fossil *P. dissecta.*

Sycamore commonly frequents valley bottoms and river banks throughout its range, and a similar habitat is suggested by its abundance at Black Hawk Ranch. It may be noted that *P. dissecta* occurs abundantly in the transitional Mio-Pliocene Neroly flora 12 miles north (Condit, 1938), where it also occupied a flood-plain habitat. But by Mulholland time, this characteristic Miocene sycamore was replaced in the lowlands of this region by the slender-lobed and entire-margined *P. paucidentata.* There is definite evidence here of an important change in climate in west-central California directly after the Black Hawk Ranch stage.

Populus washoensis is now known from a number of Middle and Upper Miocene floras in the northern Great Basin. Here it is a member of the temperate Miocene forest and is associated commonly with *Platanus dissecta,* which occurs also at Black Hawk Ranch. *Populus washoensis* closely resembles the leaves of the modern *P. grandidentata* of eastern North America. This poplar ranges from Quebec southward through the mountains into North Carolina and Virginia and thence westward into Ohio. Its regular associates include many species of the eastern deciduous forest that have close counterparts in the Miocene of western North America.

Populus washoensis is represented also in the Mulholland flora, which is described in the next chapter of this volume. The single Mulholland specimen is somewhat smaller than the average for the Black Hawk Ranch material, and it also seems to have a thicker texture. Should further collections in the Pliocene of western North America show that there is a small-leafed species related to *P. washoensis* and *P. grandidentata,* it will assume considerable paleoecological significance. A trend toward the development of smaller and thicker-textured leaves is a common characteristic of many broad-leafed deciduous genera in the later Tertiary. Two Pliocene species of *Populus* have already been distinguished on this basis from related Miocene species, and their importance has been discussed by Chaney (1938*a,* pp. 212–213). In brief, the Pliocene species most closely resemble leaves produced by their modern relatives in the drier and more southerly parts of their distribution. Their Miocene relatives, on the other hand, have leaves of larger size and thinner texture, like those found on the same modern species in the more humid parts of their ranges. A recognition of such changes in leaf size and texture in response to altered environments is of utmost importance to an interpretation of Miocene and Pliocene floras. A small-leafed poplar of the *washoensis* type is fully to be expected at Mulholland in view of the semiarid climate of that flora. In other words, there is a further suggestion here of marked changes in physical conditions in this region immediately following Black Hawk Ranch time.

Ulmus californica Lesquereux is abundant in the Black Hawk collections. This elm is now known from floras of transitional Mio-Pliocene age in the central Sierra Nevada, as set forth by Condit in chapters 2 and 3 of this volume,

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and has been recognized also by Chaney in the Lower Pliocene floras of Oregon which he discusses in chapters 11 and 12. It is related to *U. speciosa* Newberry, which is known from a number of Upper Oligocene and Miocene floras in the northern Great Basin and Columbia Plateau. This species differs from *U. californica* in its greater size and in a more frequent tendency toward asymmetry. Both species are related to the modern *U. americana* of eastern North America. *Ulmus speciosa* most nearly resembles the leaves formed by *americana* in the more humid parts of its distribution at the east, where it has both a flood-plain and an upland-slope occurrence. *Ulmus californica* is essentially like the leaves of *americana* in the more western parts of its distribution, in Nebraska, Kansas, and Oklahoma, where it has a flood-plain occurrence in a more semiarid climate. The change from the larger-leafed *U. speciosa* of the Miocene, which inhabited valley bottoms and upland slopes, to the smaller-leafed *U. californica* of the later Tertiary, with a largely riparian occurrence, may be interpreted as a change from the mild and humid conditions of the Miocene to a more continental type of climate later in the Tertiary.

These species of *Platanus, Populus,* and *Ulmus* having equivalents in the Black Hawk Ranch flora all occur in regions where 30 to 40 inches of rainfall are distributed throughout most of the year, and where extremes of temperature are moderate. The equivalent fossil species form part of the characteristic East American and East Asian Elements which occurred at the north in the Middle Tertiary as a part of the Arcto-Tertiary Flora (Chaney, 1936*b*, 1940), and which had shifted southward into west-central California before the end of that epoch.

Only *Salix hesperia* of the flood-plain group in the Black Hawk Ranch flora has no distinctive climatic or stratigraphic significance. It is one of the members of the Arcto-Tertiary Flora that has survived down to the present in scarcely modified form on the Pacific coast, where it is represented by *S. lasiandra.*

Modern descendants of the subordinate woodland-chaparral group in the Black Hawk Ranch assemblage all live in close proximity in interior southern California, where precipitation ranges from 18 to 20 inches yearly. All of them may be seen in the vicinity of Monrovia and Pasadena, where the oaks form a savanna community in the lowlands, with members of the chaparral group near by. Two of these equivalent species, *Cercocarpus betuloides* and *Quercus agrifolia,* range today into the general region of the fossil locality, whereas *Quercus engelmannii* and *Rhus ovata* do not. Largely of Middle Tertiary north Mexican (Madro-Tertiary) origin, this group, together with many species whose closest modern descendants are now of southern distribution, migrated northward into central California in later Tertiary time (Axelrod, 1939, pp. 49–58). The presence of this Southwest American Element in the flora suggests a degree of aridity in the adjacent hilly and upland areas sufficient to confine members of the flood-plain group to river banks and lowland valleys.

A habitat of this general type may be seen today in the Edwards Plateau of western Texas. The broad river valleys extending into this region from the east support a dense flood-plain community of regular members of the hardwood-deciduous forest which attains optimum development at the east, where rainfall

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is heavier and summer temperatures are lower. Included here are species of *Platanus, Populus, Salix,* and *Ulmus* that are represented by somewhat similar plants in the Black Hawk Ranch assemblage. It is significant that leaves and other structures from this flood-plain community dominate contemporary deposits along rivers in the region. The adjacent rolling hills and uplands are characterized by oak-juniper woodland, but the latter's contribution to accumulating deposits along the rivers is definitely subordinate as compared with that of the flood-plain community. The presence of a high water table in the river valley largely restricts the oak-juniper community away from immediate sites of deposition, and this same factor may account for its rarity at Black Hawk Ranch. The species of *Cercocarpus, Quercus,* and *Rhus* in this woodland resemble the Black Hawk Ranch fossils, but they are not so closely related as the California species listed on page 92. The relationships between modern species characterizing the flood-plain and woodland communities in the Edwards Plateau and the Black Hawk Ranch fossils may be expressed as follows:

Fossil species	*Related species in the Edwards Plateau, Texas*
Mesic flood plain	
Platanus dissecta	P. occidentalis Linnaeus
Populus washoensis	P. deltoides Marshall
Salix hesperia	S. amygdaloides Andersson
Ulmus californica	U. americana Linnaeus
Woodland-chaparral	
Cercocarpus cuneatus	C. montanus Rafinesque
Quercus convexa	Q. oblongifolia Torrey
Quercus lakevillensis	Q. grisea Liebmann
Rhus moragensis	R. virens Lindheimer

The significance of this relationship between the Black Hawk Ranch flora and vegetation living in western Texas is actually greater than is apparent from this list alone. The woodland-chaparral communities of California and western Texas are related historically, for both are late Cenozoic segregates of the generalized Madro-Tertiary Flora. As might be expected from such a relationship, there are now known to be a number of Miocene and Pliocene species in California whose nearest descendants survive in the woodland which occupies the region from the Edwards Plateau southward into the Sierra Madre Oriental of Mexico. These descendants include such species as:

Forestiera reticulata Torrey
Pistacia mexicana Humboldt, Bonpland, and Kunth
Quercus fusiformis Small
Quercus vaseyana Buckley
Rhus lanceolata (Gray) Britton
Ungnadia speciosa Endlicher

There are other woodland-chaparral species in the later Tertiary of central California with surviving equivalents ranging from southern Arizona to Texas and southward into Mexico. Among these are *Robinia neo-mexicana* Gray and *Sapindus drummondii* Hooker and Arnott. In instances where Californian

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species seem most nearly related to the fossils, there often are closely similar species in the same genera at the east: *Arbutus, Ceanothus, Cercocarpus, Garrya, Juglans, Juniperus, Platanus, Quercus,* and *Rhus.* In other cases, the same species ranges from California to Texas, as with *Arctostaphylos pungens* Humboldt, Bonpland, and Kunth, *Celtis reticulata* Torrey, *Mahonia fremontii* (Torrey) Fedde, or *Rhamnus californica* Eschscholtz. It must be emphasized that all these plants having equivalents in later Tertiary floras in California live in close proximity to the hardwood-deciduous flood-plain community including modern equivalents of the East American Element in the Edwards Plateau and in the Sierra Madre Oriental at the south. The overlap of close representatives of the Southwest American and East American Elements in these areas has definite historical significance. It duplicates in some measure conditions found in central California during the later Tertiary, when the Madro-Tertiary Flora ranged northward to make contact with the Arcto-Tertiary Flora, which has a large East American Element.

This fact is exemplified better by the Remington Hill and Table Mountain floras, described by Condit in chapters 2 and 3 of this volume, and to a lesser extent by the Mulholland flora, described in chapter 5, than by the Black Hawk Ranch. But this degree of difference may be more apparent than real, for these floras have four to five times as many species as the Black Hawk Ranch. Evidence drawn from several undescribed early Pliocene flood-plain assemblages in central California (Diablo, Jacalitos, San Joaquin) suggests a closer relationship to modern vegetation of the region from the Edwards Plateau southward into the Sierra Madre Oriental than is displayed by the Remington Hill and Table Mountain floras, which contain a large West American Element.

With respect to the physical conditions of Black Hawk Ranch time, the proximity of an arid community on hills adjacent to the Black Hawk Ranch area indicates that the flood-plain species were living in a region of lower rainfall than during the Miocene, for typical Miocene floras of this and other regions to the north contain no such group. It would appear that the flood-plain community was living under conditions where distribution is controlled largely by compensatory factors (Rübel, 1935). Owing to the coastal position of the locality, these are thought to have involved a low evaporation rate, moderate ranges of temperature, and ameliorating ocean breezes, for conditions at the interior were definitely arid in the Pliocene (Axelrod, 1940*a–d*). In this connection it may be noted that an analogous situation existed in coastal regions during the Miocene. Chaney has shown that warm-temperate Eocene relicts such as *Persea* and *Sabalites* survived into the Miocene in coastal Oregon when that region was dominated by a temperate redwood forest (1938*c*, p. 641). The Neroly *Taxodium-Nyssa* community shows a similar mixture, for it contains *Persea, Magnolia,* and *Tetracera.* These relationships are closely duplicated today in the modern flora of Louisiana and Florida, where most of the same warm-temperate genera have survived near the coast under the influence of a mild oceanic climate. A somewhat different aspect is represented by the Mio-

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Pliocene Puente flora of southern California, which shows such relicts of the Caribbean Element as *Anona, Ficus, Persea, Ocotea,* and *Magnolia* surviving in a region then dominated by live oaks and their semiarid associates (Axelrod, 1939, pp. 55, 68–69); this relationship is shown also by the Upper Miocene Monterey flora at Carmel, now being studied by Oliver. Modern vegetation resembling these floras persists in mountain valleys along the coasts of northern Mexico from Nuevo León southward to Vera Cruz, and from Sinaloa southward into Jalisco. All these occurrences of warmer Eocene relicts surviving in regions inhabited by both temperate and relatively semiarid floras are explainable on the basis of the compensatory conditions provided by a coastal location. It is believed that the dominant flood-plain group of the Black Hawk Ranch flora likewise persisted into the Pliocene owing to favorable and local coastal conditions. This interpretation finds support also in the absence of such communities at this latitude over lowland areas at the interior during the Pliocene.

From the foregoing discussion it is clear that Miocene and derivative Miocene species of flood-plain character dominated the lowlands of the Mount Diablo region during Lower Pliocene time. But this assemblage is less mesic than the *Taxodium-Nyssa* community which characterized the lowlands of this region in preceding Neroly time. In addition to the bald cypress and tupelo gum, the Black Hawk Ranch also lacks the species of *Persea, Magnolia, Smilax,* and *Tetracera* which survived in this region into latest Miocene time. The absence of these and similar types at Black Hawk Ranch, and the presence of a derivative Miocene elm, *Ulmus californica,* suggests greater extremes of temperature and a lower rainfall than during the preceding Neroly stage. The presence of semiarid woodland-chaparral plants on near-by upland slopes in Black Hawk Ranch time leads to a similar conclusion, since these types have not been recorded in the Neroly. They indicate that the trend to aridity in this region had progressed sufficiently by Black Hawk Ranch time to permit members of the Madro-Tertiary Flora to invade this coastal region from drier inland areas (Axelrod, 1938, 1939, 1940*b*). Annual precipitation during the Black Hawk Ranch stage probably was in the neighborhood of 25 inches. The dominance of species in the flora having their closest modern representatives in areas with summer rains suggests that precipitation occurred during the summer as well as the winter months. Summer temperatures must have been considerably more moderate than those now prevailing in the region, and as a result, evaporation was much lower.

Age of the Flora

Discussion of the relationships of the Black Hawk Ranch flora to the other Pliocene floras in this region will be delayed to a later chapter in the present volume (chap. 8), to include floras which have a direct bearing on an interpretation of the changing physical conditions in west-central California during the later Tertiary. It is sufficient to indicate here that a comparison with the Mio-Pliocene Neroly flora (Condit, 1938) on the one hand, and the early Middle

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Pliocene Mulholland on the other, demonstrates that the Black Hawk Ranch flora is essentially intermediate in its composition, and that it is accordingly of Lower Pliocene age.

The occurrence of the flora in an exceptionally rich vertebrate quarry permits the closer placing of its age. The Black Hawk Ranch fauna, which is of mid-Lower Pliocene age, is being studied by Richey, who has already published several preliminary statements on its composition and relationships (1938, 1940).

Summary

The predominantly Miocene aspect of the Lower Pliocene Black Hawk Ranch flora is ascribed to locally persistent moderate conditions provided by a coastal location. This relict occurrence is to be expected during such an epoch as the Pliocene, when topographic diversity and micro-climates controlled the distribution of vegetation essentially as they do today.

The Black Hawk Ranch, as well as certain other later Tertiary floras in central California, shows relationship to woodland-chaparral and hardwood-deciduous flood-plain vegetation living in close proximity in the Edwards Plateau of Texas and in the Sierra Madre Oriental of Mexico. Environmental conditions in these areas closely resemble those existing in central California in later Tertiary time, when the Madro-Tertiary bordered the Arcto-Tertiary Flora, which has a large East American Element.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA

Class ANGIOSPERMAE

Subclass DICOTYLEDONES

Family SALICACEAE

Populus washoensis Brown

(Plate 22, figures 1, 2)

Populus washoensis Brown, Jour. Wash. Acad. Sci., vol. 27, p. 516, 1937 (see synonymy). H. V. Smith, Bull. Torrey Bot. Club, vol. 66, p. 467, pl. 10, fig. 1, 1939.

Populus lindgreni Knowlton. Oliver (in part), Carnegie Inst. Wash. Pub. 455, p. 17, specimen 661 only, 1934.

This poplar has been recorded from the Upper Cedarville flora of northwestern Nevada, the Blue Mountains flora of Oregon, and the Thorn Creek and Succor Creek in southern Idaho. It is represented also in a recently collected Truckee flora at Chalk Hills, near Virginia City, Nevada, and in the San Joaquin formation near Coalinga; these floras are respectively of Lower and Upper Pliocene age.

The closely related living species *Populus grandidentata* Michaux grows in moist sandy soils near streams and is common throughout eastern United States.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1736, 1737; no. 1738.

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Salix hesperia (Knowlton) Condit

(Plate 22, figure 3)

Salix hesperia (Knowlton) Condit, Carnegie Inst. Wash. Pub. 553, pp. 41–42, pl. 4, fig. 7, 1944 (see synonymy and discussion).

Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

Several fragmentary willow leaves show sufficient diagnostic characters to permit their reference to this common Miocene species, which is related to the modern *Salix lasiandra* Bentham of the Pacific coast. The specimen figured represents a group of capsules.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1739; no. 1740.

Family FAGACEAE

Quercus convexa Lesquereux

Quercus convexa Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 4, pl. 1, figs. 13–17, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 76, pl. 14, figs. 2, 3, 5, 6, 1944 (see synonymy).

A single impression of an oblong live-oak leaf can be referred to this species, which is considered to be the fossil equivalent of the modern *Quercus englemannii* Greene of southern California. This is another member of the semiarid woodland which migrated into central California in early Pliocene time from a Middle Tertiary north Mexican center of distribution.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1741.

Quercus lakevillensis Dorf

Quercus lakevillensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 82–84, pl. 8, figs. 4, 5, 1930.

Two leaf specimens closely resemble the modern *Quercus agrifolia* Née of California. Still unrecorded from the continental Miocene floras, this species may have had a southern interior origin, or may possibly be referable to a maritime source together with the closed-cone pine forests.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1742.

Family ULMACEAE

Ulmus californica Lesquereux

(Plate 22, figures 4, 5)

Ulmus californica Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. 7*a*, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 46, pl. 8, fig. 4, 1944 (see synonymy).

Large symmetrical and asymmetrical elm leaves with doubly serrate teeth are common in the flora, and are easily identified as *Ulmus californica*. This species differs from the related Miocene *U. speciosa* Newberry in having typically smaller leaves. Whereas specimens of *U. californica* resemble the smaller leaves produced by the living *U. americana* Linnaeus in the drier parts of its range west of the Mississippi River, those of *U. speciosa* are larger and more nearly like the leaves formed by that species in the humid parts of its distribution in the eastern United

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States. It is evident that *U. californica* may be regarded as another derivative Miocene species showing leaf modification in response to the development of a drier and cooler climate in the western United States during the later Tertiary (Chaney, 1938*a*, pp. 212–213).

Also included in the collection are slender asymmetrical elm leaves which may be single-serrate or may have small subsidiary teeth. Some of these were at first considered to be *Ulmus brownellii* Lesquereux and *Zelkova oregoniana* (Knowlton) Brown, but they are now believed to represent variation in *U. californica*. This conclusion was suggested by the fact that leaves of both types have been noted on *Ulmus americana* in Berkeley, California.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1743, 1746; nos. 1744, 1745, 1747, 1748, 1749.

Family PLATANACEAE

Platanus dissecta Lesquereux

(Plate 22, figure 6; plate 23)

Platanus dissecta Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 13, pl. 7, fig. 12; pl. 10, figs. 4, 5, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 80–81, pl. 15, figs. 1, 4, 1944 (see synonymy).

The leaves of *Platanus dissecta* may be differentiated from those of *P. paucidentata* Dorf and *P. aceroides* Goeppert by evaluating them on the basis of their margin, lobing, and shape. Any one of these characters alone may be insufficient, but recognition of all of them together provides in most cases a satisfactory basis for species differentiation. The leaves of *P. dissecta* have teeth which are typically subfalcate and large, and sinuses which are mostly of moderate depth. *Platanus paucidentata* often has an entire margin, which has not been noted in *P. dissecta*. When teeth occur in *P. paucidentata* they are typically subordinate, but in some cases they approach the subfalcate condition; in such instances the leaves may be differentiated from those of *P. dissecta* by their deeper sinuses. The leaves of *P. dissecta* may be of nearly equal dimensions, but in most cases they are of greater length than width. *Platanus paucidentata*, on the other hand, has typically a greater width than length, and the sinuses are narrower than in *P. dissecta*. *Platanus aceroides* may be distinguished from both *P. paucidentata* and *P. dissecta* by its more shallow lobes.

The relationships of *P. paucidentata* and *P. aceroides* to the living *P. racemosa* and *P. occidentalis* seem satisfactorily established, but *P. dissecta* apparently has no close counterpart in the modern flora. MacGinitie (1937, pp. 140–141) has considered that it most nearly resembles *P. orientalis*, but the writer has not had access to sufficient material of this species to make comparison with *P. dissecta*. As judged from the herbarium material examined, *P. dissecta* seems to be somewhat intermediate between *P. orientalis* and *P. racemosa*. Regardless of its exact modern affinities, it is clear that *P. dissecta* was a regular member of the temperate Miocene forest of the western United States, and that it has no close counterpart in the modern flora of the Pacific states.

Specimens of *P. dissecta* recorded from certain northern Miocene localities (Latah, Grand Coulee, St. Eugene silts) have consistently greater dimensions than those from the Table Mountain and Black Hawk Ranch localities. Considered alone, the differences between these California and Washington–British Columbia localities are sufficient to warrant recognition of the northern species as distinct from *P. dissecta*.

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It must be noted, however, that floras which occupy an intermediate position geographically (Mascall, Succor Creek, Austin-Tipton) show characters which overlap the Washington and California specimens. Whether there are sufficient differences to distinguish the sycamores of these three areas is here left an open question. It is certain that large collections must be made from many localities before this problem can be settled satisfactorily.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1751, 1752; no. 1753.

Family ROSACEAE

Cercocarpus cuneatus Dorf

Cercocarpus cuneatus Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 98–99, pl. 12, fig. 3, 1930. Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 175–176, pl. 4, fig. 4, 1937.

A single leaf impression is assigned to this Pliocene species, which closely resembles the modern *Cercocarpus betuloides* Nuttall, a common member of the chaparral formation of California.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1750.

Family ANACARDIACEAE

Rhus moragensis Axelrod

Rhus moragensis Axelrod, Carnegie Inst. Wash. Pub. 553, p. 141, pl. 31, figs. 7, 9, 1944.

A single leaf impression clearly represents this evergreen sumac, which is described in the Mulholland flora (chap. 5 below). It differs from the type material in the nature of the secondaries, which tend to loop along the margin, rather than typically bifurcating and entering it. That this specimen is properly referable to *Rhus moragensis* is shown by the fact that the leaf venation of its modern equivalent, *Rhus ovata* Watson, may be of either the Mulholland or the Black Hawk type (see University of California Herbarium sheets 124174, 499695).

Rhus ovata is a common chaparral species in southern California and occurs also in southern Arizona. The Pliocene record of its fossil equivalent in central California is regarded as another example of the northward movement of the Madro-Tertiary Flora in the early Pliocene, and its restriction southward later in the epoch.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1754.

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PLATES 22, 23

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PLATE 22

Black Hawk Ranch fossils

PAGE

Figs. 1, 2. *Populus washoensis* Brown. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1737, 1736 98

Fig. 3. *Salix hesperia* (Knowlton) Condit. Fruits. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1739 99

Figs. 4, 5. *Ulmus californica* Lesquereux. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1746, 1743 99

Fig. 6. *Platanus dissecta* Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1752 100

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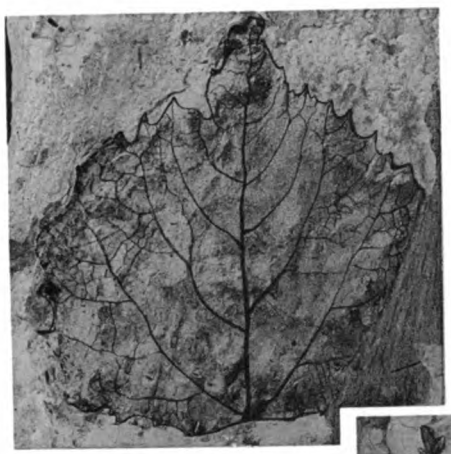

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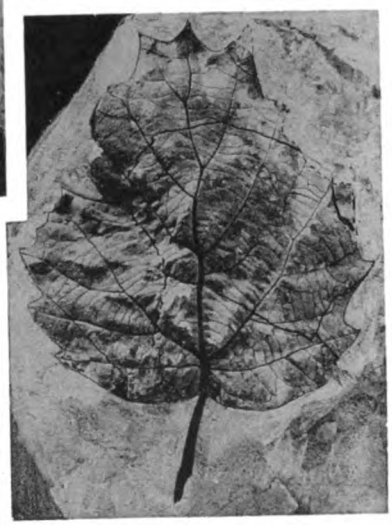

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PLATE 23

Black Hawk Ranch fossils

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Platanus dissecta Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1751 100

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5

The Mulholland Flora

DANIEL I. AXELROD

Introduction

The collection and study of later Tertiary floras in the western United States has been occupying the writer's attention for the past ten years. A number of new floras from the Pliocene of California which are now being studied will materially supplement our knowledge of the vegetation of this epoch, which was described first by Dorf over a decade ago (1930). In addition to these new floras, collections have also been made at some of the horizons previously reported by Dorf. The most important of the latter is in the Pliocene continental sediments of the eastern Oakland-Berkeley Hills, and is described in the present report. This flora, which is termed the Mulholland (Stirton, 1939*a*, p. 388), comes from the St. Mary's locality described by Dorf (locality 162), and includes additional material collected from the adjacent strata.

The following 9 species were recorded originally from this deposit:

Platanus paucidentata Dorf
Populus alexanderi Dorf
Populus prefremontii Dorf
Prunus merriami Dorf
Quercus hannibali Dorf
Quercus orindensis Dorf
Rhus sp. Dorf
Salix coalingensis Dorf
Salix sp. Dorf

From a consideration of the distribution of the most closely related modern equivalents of these plants, and from a comparison with other Pliocene floras in the region, Dorf reached the following important conclusions regarding this florule: (1) The fossil assemblage shows a relationship to vegetation now occurring in southern California. (2) There has been an increase in rainfall since the time of floral deposition. (3) The semiarid aspect of the flora is consistent with its Middle Pliocene age.

The first additional collections from this locality were made by H. L. Mason during 1931, when road construction made new exposures available. The writer has determined 16 additional species from this collection, bringing the total to 25 at this locality. Two new deposits directly north of this outcrop were discovered in embankments along the Sacramento Northern Railway during the spring of 1938 by Sam Johnson, a student in paleontology at the University of California. Further collections here have yielded 43 species, including all 25 from the original locality.

The Mulholland, consisting of 2200 specimens, represents by far the largest collection from any one Pliocene flora known in North America, and adds a

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critical chapter to later Tertiary paleobotany. In addition to substantiating the conclusions drawn by Dorf, our present knowledge of this flora gives an increasingly complete picture of the environment in the region, and aids also in explaining certain peculiar facts of plant distribution in California. Finally, it adds support to the belief that members of a semiarid Southwest American Element invaded central California during early Pliocene time (Axelrod, 1938, 1939).

Geologic Occurrence

The sediments at the plant locality were mapped originally as the Orinda formation (Lawson, 1915). During recent years, however, the Orinda has been shown to be limited to the Berkeley Hills (Clark, 1933; Richey, 1939), where it rests unconformably upon the Miocene Monterey formation. Vertebrate and invertebrate fossils from the true Orinda represent the *Nannippus tehonensis* zone, as well as the Neroly stage of the San Pablo group (Richey, 1937). Conformably overlying the Orinda are the Moraga and Siesta formations (Lawson, 1915), both of which contain Lower Pliocene vertebrates (Stirton, 1939*a*). The three formations are exposed in a syncline whose axis lies just east of the crest of the Berkeley Hills, and they are cut off along the east front of the range by the Moraga fault (Clark, 1933). The continental sediments to the east have a thickness of over 4000 feet and have been termed the Tassajero formation (*ibid.*). They contain almost no lavas, and tuff beds are lacking except in the lower part of the formation. These sediments not only differ in lithology from the Orinda, as was originally pointed out by Lawson and Palache (1902, p. 396), but are younger.

The type section of the Tassajero formation lies along Tassajero Creek on the southwestern slope of Mount Diablo, 15 miles distant from the Mulholland locality, and separated from it by Las Trampas Ridge, which attains an elevation of 1800 feet. Although it has not been possible to trace the Tassajero westward into the Mulholland region, it may be noted that there is a general lithological similarity and that the age relations in the two areas appear to agree. The Middle Pliocene Tassajero grades downward into the continental sediments containing the Lower Pliocene Black Hawk Ranch fauna, and the sediments at Mulholland, which contain Middle Pliocene vertebrates, are underlain to the southeast by beds of approximately Black Hawk age (Stirton, 1939*a*, pp. 341, 366, maps).

Other than to point out this probable correlation of the Mulholland with the Tassajero, it does not seem desirable to consider the relations of these continental deposits in more detail at this time. Although the sediments may be divided into floral and faunal zones, the criteria for areal mapping are still in the process of being assembled. In the Mount Diablo area there is evidence of nearly continuous deposition throughout the Pliocene, representing an accumulation of over 7000 feet. In the region of the fossil locality the sediments exceed 4000 feet in thickness and have been folded and faulted. In both areas it is difficult to trace members for any distance.

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The Mulholland flora comes from two important localities in the area directly northeast of St. Mary's College.

Locality 162. Dorf's locality is exposed on a road cut ¾ mile north of St. Mary's College. Most of the material comes from the northeast corner of the junction of the county road and a road which runs southeasterly along Las Trampas Creek past the college reservoir.

Locality P386. (See plate 24.) Leaf impressions occur in the first and third railroad cuts north of the county road crossing the Sacramento Northern Railway directly northeast of St. Mary's College. The two leaf-bearing horizons are separated by about 300 feet of gray to yellow-brown shales and sandstones and pebble beds, and are approximately 2000 feet above the base of the formation, which here rests on the Neroly. The uppermost horizon is within 150 yards of locality 162 and represents an extension of the same strata. Since the floras at the two localities are essentially similar, they will be treated together.

Composition and Physical Indications

The flora consists of 43 angiosperms, which are distributed among 30 genera and 19 families. Ten species are described as new, and the remainder are referred to plants recorded previously in the Miocene and Pliocene floras of the western United States; 1 of the latter has been given a new name and 1 is described as a new combination.

Systematic List of Species

Spermatophyta
- Angiospermae
  - Monocotyledones
    - Pandanales
      - Typhaceae
        - Typha lesquereuxi Cockerell
    - Graminales
      - Gramineae
        - Poacites sp.
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Populus alexanderi Dorf
        - Populus parce-dentata (Lesquereux) new combination
        - Populus prefremontii Dorf
        - Populus washoensis Brown
        - Salix hesperia (Knowlton) Condit
        - Salix wildcatensis new name
    - Fagales
      - Betulaceae
        - Alnus merriami Dorf
      - Fagaceae
        - Castanopsis perplexa (Knowlton) Brown
        - Quercus bockéei Dorf

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- Quercus declinata Dorf
- Quercus moragensis new species
- Quercus orindensis Dorf
- Quercus simulata Knowlton
- Quercus wislizenoides new species

Urticales
- Ulmaceae
  - Celtis kansana Chaney and Elias

Ranales
- Berberidaceae
  - Mahonia marginata (Lesquereux) Arnold
- Lauraceae
  - Umbellularia salicifolia (Lesquereux) Axelrod

Papaverales
- Papaveraceae
  - Dendromecon reticulata new species

Rosales
- Platanaceae
  - Platanus paucidentata Dorf
- Rosaceae
  - Amelanchier sp. Dorf
  - Cercocarpus cuneatus Dorf
  - Chamaebatia prefoliolosa Brown
  - Lyonothamnus mohavensis Axelrod
  - Photinia sonomensis new species
  - Prunus moragensis new species
  - Prunus prefasciculata Axelrod

Sapindales
- Anacardiaceae
  - Rhus franciscana new species
  - Rhus moragensis new species
  - Rhus prelaurina Axelrod
- Aceraceae
  - Acer bolanderi Lesquereux
- Sapindaceae
  - Sapindus oklahomensis Berry

Rhamnales
- Rhamnaceae
  - Berchemia multinervis (Al. Braun) Heer
  - Ceanothus prespinosus new species
  - Rhamnus moragensis new species
  - Rhamnus precalifornica Axelrod

Malvales
- Sterculiaceae
  - Fremontia lobata Axelrod

Umbellales
- Cornaceae
  - Cornus ovalis Lesquereux
  - Nyssa elaenoides (Lesquereux) Condit

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Ericales
  Ericaceae
    Arbutus matthesii Chaney
    Arctostaphylos moragensis new species
Gentianales
  Oleaceae
    Fraxinus caudata Dorf

Table 11 shows the relative abundance of the species in the flora. Oaks clearly dominate the assemblage, and 2 of them, *Quercus wislizenoides* and *Q. orindensis,* are among the commonest species; together they account for 39 per cent of the flora. The next 10 species, *Platanus paucidentata, Populus prefremontii, Salix wildcatensis, Quercus moragensis, Typha lesquereuxi, Sapindus oklahomensis, Quercus declinata, Poacites sp., Salix hesperia,* and *Photinia sonomensis,* account for another 54 per cent of the flora, with the first 3 totaling 38 per cent. None of the remaining 31 species is common, the majority being represented by less than 5 specimens.

The methods commonly employed in attempting to reconstruct Tertiary floras have been restated by Chaney in two recent papers (1936*b*, 1938*b*). It is only necessary to reiterate here that any attempt to interpret past climate and environment must first involve a comparison of the fossil flora with the modern vegetation which resembles it most closely. Although it is not possible in some cases to duplicate an older Tertiary flora among living forests, or to visualize the conditions under which it existed, such difficulties are rarely met in a study of Pliocene floras. These later Tertiary assemblages in the western United States closely resemble vegetation living at no great distance from the fossil localities. Since Pliocene species do not differ greatly from modern plants, it is possible to determine with reasonable accuracy the physical conditions under which they lived.

The Mulholland species may be divided into the floral elements and components listed in table 12. Their relative percentages, as gauged from the abundance of the species,[1] may be expressed as follows:

	Per cent
Southwest American Element	
Oak woodland Component	83.9
Chaparral Component	4.1
West American Element	
Border-redwood Component	10.8
Sierra-Cascade Component	0.2
Rocky Mountain Component	0.4
East American Element	0.4
East Asian Element	0.2
	100.0

[1] From these totals, *Typha lesquereuxi* and *Poacites* sp. are omitted because their modern equivalents are too widely distributed to be significant.

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TABLE 11

RELATIVE ABUNDANCE OF SPECIES IN THE MULHOLLAND FLORA

Species	*Number of specimens*	*Per cent*
Quercus wislizenoides	680	30.9
Platanus paucidentata	355	16.1
Populus prefremontii	343	15.5
Quercus orindensis	176	8.0
Salix wildcatensis	151	6.8
Quercus moragensis	95	4.3
Typha lesquereuxi	61	2.7
Sapindus oklahomensis	60	2.7
Quercus declinata	49	2.2
Poacites sp.	36	1.6
Salix hesperia	34	1.5
Photinia sonomensis	22	1.0
Fremontia lobata	19	0.8
Rhus prelaurina	14	0.6
Rhamnus precalifornica	14	0.6
Umbellularia salicifolia	13	0.6
Rhus moragensis	8	0.4
Ceanothus prespinosus	8	0.4
Acer bolanderi	7	0.4
Cercocarpus cuneatus	5	0.3
Berchemia multinervis	4	0.2
Lyonothamnus mohavensis	4	0.2
Quercus simulata	4	0.2
Prunus prefasciculata	4	0.2
Castanopsis perplexa	3	0.2
Populus parce-dentata	3	0.2
Celtis kansana	3	0.2
Prunus moragensis	3	0.2
Populus alexanderi	2	0.7
Alnus merriami	2	
Rhus franciscana	2	
Cornus ovalis	2	
Arbutus matthesii	2	
Fraxinus caudata	2	
Mahonia marginata	2	
Amelanchier sp.	1	
Chamaebatia prefoliolosa	1	
Dendromecon reticulata	1	0.3
Arctostaphylos moragensis	1	
Populus washoensis	1	
Quercus bockéei	1	
Nyssa elaenoides	1	
Rhamnus moragensis	1	
Total	2200	100.0

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TABLE 12

ELEMENTS AND COMPONENTS OF THE MULHOLLAND FLORA

Fossil species	*Equivalent living species*
Southwest American Element	
Oak woodland Component	
Celtis kansana	C. reticulata Torrey
Lyonothamnus mohavensis	L. floribundus Gray
*Platanus paucidentata	P. racemosa Nuttall
Populus prefremontii	P. fremontii Watson
Prunus prefasciculata	P. fasciculata Gray
Quercus declinata	Q. tomentella Engelmann
Quercus moragensis	Q. lobata Née
Quercus orindensis	Q. vaseyana Buckley
Quercus wislizenoides	Q. wislizenii A. DeCandolle
Salix wildcatensis	S. lasiolepis Bentham
Sapindus oklahomensis	S. drummondii Hooker and Arnott
Chaparral Component	
Arctostaphylos moragensis	A. glandulosa Eastwood
Ceanothus prespinosus	C. spinosus Nuttall
Cercocarpus cuneatus	C. betuloides Nuttall
Dendromecon reticulata	D. rigida Bentham
Fremontia lobata	F. californica Torrey
Mahonia marginata	M. fremontii (Torrey) Fedde
Photinia sonomensis	P. arbutifolia Lindley
Rhamnus moragensis	R. crocea Nuttall
Rhamnus precalifornica	R. californica Eschscholtz
Rhus moragensis	R. ovata Watson
Rhus prelaurina	R. laurina Nuttall
West American Element	
Border-redwood Component	
Alnus merriami	A. rhombifolia Nuttall
Amelanchier sp	A. alnifolia Nuttall
Arbutus matthesii	A. menziesii Pursh
Cornus ovalis	C. californica C. A. Mey
Fraxinus caudata	F. oregona Nuttall
*Platanus paucidentata	P. racemosa Nuttall
Populus alexanderi	P. trichocarpa Torrey and Gray
Prunus moragensis	P. emarginata (Douglas) Walpers
Rhus franciscana	R. diversiloba Torrey and Gray
Salix hesperia	S. lasiandra Bentham
Umbellularia salicifolia	U. californica Nuttall
Sierra-Cascade Component	
Castanopsis perplexa	C. sempervirens Dudley
Chamaebatia prefoliolosa	C. foliolosa Bentham
Rocky Mountain Component	
*Acer bolanderi	A. grandidentatum Nuttall
Populus parce-dentata	P. acuminata Rydberg
East American Element	
*Acer bolanderi	A. grandidentatum Nuttall
Berchemia multinervis	B. scandens Trelease
Nyssa elaenoides	N. sylvatica Marshall
Populus washoensis	P. grandidentata Michaux
East Asian Element	
Quercus bockéei	Asiatic Fagaceae
Quercus simulata	Q. myrsinaefolia Blume

*Species occurring in more than one component.

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In order to reconstruct the physical conditions of Mulholland time, it is evident that major attention must be directed to regions where living equivalent species of the dominant Oak woodland Component are bordered by those of the Chaparral and Border-redwood.

Equivalents of members of the Oak woodland, Chaparral, and Border-redwood Components form a characteristic part of the vegetation of central and southern California at low to moderate elevations. Of the 41 woody plants in the Mulholland flora, the 32 characterizing these components have modern representatives in California, and 22 of these live within a few tens of miles of the fossil locality. Modern equivalents of 5 Mulholland dominants, *Platanus racemosa, Populus fremontii, Quercus lobata, Q. wislizenii,* and *Salix lasiolepis,* live in close association on Mount Diablo 15 miles east of the fossil locality, where annual rainfall is lower and temperatures are higher in summer. The oaks form a savanna over the lower flanks of the mountain, with willow, cottonwood, and sycamore common along the streams. Digger pine, *Pinus sabiniana* Douglas, is common in the woodland but is not known to have an equivalent in the Mulholland flora. One of its regular associates, *Quercus douglasii* Hooker and Arnott, may be considered an ecological equivalent of another Mulholland dominant, *Q. orindensis,* which seems more nearly related to *Q. vaseyana* of the southwestern United States. Chaparral is common over the middle and upper slopes of the mountain, and contains such equivalents of Mulholland species as *Arctostaphylos glandulosa, Cercocarpus betuloides, Dendromecon rigida, Fremontia californica, Rhamnus californica,* and *R. crocea.* Besides forming distinct associations on the more exposed slopes, these shrubs often are scattered through the oak woodland. They also are found frequently in the border-redwood forest that is restricted to deep canyons on the lower and middle flanks of the mountain. On Mount Diablo representatives of the Border-redwood Component include such species as *Alnus rhombifolia, Amelanchier alnifolia, Arbutus menziesii, Cornus californica, Fraxinus oregona, Prunus emarginata, Rhus diversiloba, Salix lasiandra,* and *Umbellularia californica.*

Although vegetation in the Mount Diablo region shows close relationship to the Mulholland flora, somewhat greater affinity is displayed by the living flora on the inner slopes of the Santa Cruz Mountains 40 miles southwest of the fossil locality. The general physiognomy of the vegetation in this region (pl. 25, figs. 1, 2) is considered more nearly suggestive of the Mulholland flora because equivalents of the Border-redwood Component have a more important place here than at Mount Diablo, where they are largely relict and restricted to deep canyons away from lowland depositional sites. The representation of this component in the Mulholland flora suggests that it was a well developed community in cooler canyons bordering the basin of deposition. On the leeward slopes of the southern Santa Cruz Mountains oaks form a characteristic savanna over the lower slopes and flats, with their regular riparian associates along the stream valleys. Equivalents of the Border-redwood Component, including *Alnus, Amelanchier, Arbutus, Cornus, Fraxinus, Populus, Prunus, Salix,* and *Umbellularia,* live on the cooler slopes and at higher elevations, and also descend

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to lower levels in deep canyons; thence they extend out into the broad valleys along the stream courses, where they are occasional in the oak woodland country. The exposed bordering slopes support a prominent chaparral, and its species mingle regularly with those of the border-redwood and oak woodland associations.

The 22 Mulholland plants with equivalent species now found in west-central California near the fossil locality extend into southern California, where there are 8 additional plants with representatives in the flora, *Ceanothus spinosus, Celtis reticulata, Lyonothamnus floribundus, Mahonia fremontii, Prunus fasciculata, Quercus tomentella, Rhus laurina,* and *R. ovata.* In the Santa Ynez Mountains back of Santa Barbara are the following species with equivalents in the Mulholland flora; those marked with an asterisk do not range north into central California.

Alnus rhombifolia
Amelanchier alnifolia
Arbutus menziesii
Arctostaphylos glandulosa
*Ceanothus spinosus
Cercocarpus betuloides
Cornus californica
Dendromecon rigida
Fraxinus oregona
Fremontia californica
Photinia arbutifolia
Platanus racemosa
Populus fremontii
Populus trichocarpa
Prunus emarginata
Quercus lobata
Quercus wislizenii
Rhamnus californica
Rhamnus crocea
Rhus diversiloba
*Rhus laurina
*Rhus ovata
Salix lasiandra
Salix lasiolepis
Umbellularia californica

The mountain slopes of this region are dominated by a chaparral climax (pl. 26, fig. 1). Here are to be found the species of *Arctostaphylos, Ceanothus, Dendromecon, Fremontia, Photinia, Rhamnus,* and *Rhus. Arbutus menziesii* and *Quercus wislizenii* occur near the crest of the range and extend to lower levels in deeper canyons. In these areas they are associated with such equivalent members of the Border-redwood Component as *Alnus, Cornus, Populus, Prunus, Salix,* and *Umbellularia.* The oak savanna and grassland occur regularly on flats at lower levels along the flanks of the range (pl. 26, fig. 2).

Most of these plants in the Santa Ynez Mountains also live near the fossil locality, but the physiognomy of the vegetation differs in the two areas. Whereas grassland is widespread in west-central California and chaparral is of limited occurrence, chaparral dominates the mountain slopes in southern California and grassland is limited largely to lower flats. Chaparral is an expanding climax in southern California and has displaced formerly widespread associations of savanna, woodland, and coniferous forests (Axelrod, 1937, p. 154). In central California, on the other hand, chaparral is mostly seral and subclimax in character, and as a result the other communities are developed to a greater degree. Another important difference is in the ecological relationships of the interior live oak, *Quercus wislizenii,* whose fossil equivalent, *Q. wislizenoides,* is the

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dominant species of the flora. Only in central California does it form a savanna comparable with its presumed Mulholland occurrence. In southern California it grows typically at higher elevations and in the upper parts of the chaparral.

All species in the Santa Ynez Mountains having fossil equivalents in the Mulholland flora occur on Santa Cruz Island, 30 miles distant, where the endemics *Lyonothamnus floribundus* and *Quercus tomentella* now make up a prominent part of the insular woodland. Most of the plants in the Santa Barbara coastal region also extend into interior southern California. The insular endemics are absent, but such coastal species as *Ceanothus spinosus* and *Rhus laurina* range to the interior province in the seaward-facing valleys and canyons. *Celtis reticulata, Mahonia fremontii,* and *Prunus fasciculata* are found in this interior region, and often are typical of desert-border habitats; the former two are more common in the southwestern United States (see below). Nevertheless, all these species are living with representatives of the Oak woodland, Chaparral, and Border-redwood Components in this region. Nearly all of them are found in close proximity in the mountainous areas of central San Diego and Riverside counties.

Equivalents of the Sierra-Cascade Component of the Mulholland flora, *Chamaebatia* and *Castanopsis,* find maximum expression in the Sierra Nevada. *Chamaebatia* forms dense mats in the lower part of the yellow pine forest, and extends also into the upper part of the chaparral and woodland. It is represented in San Diego County by another species, *C. australis* (Brandegee) Abrams, distinct from the Sierra Nevada and the Mulholland species. *Castanopsis* is a regular member of the conifer-chaparral association in the Sierra Nevada. In the northern part of the range and in the north Coast Ranges it overlaps another species, *C. chrysophylla* A. DeCandolle, which ranges southward into the Santa Lucia Mountains. *Castanopsis sempervirens* ranges into southern California with the Sierra-Cascade forest, and in the higher mountains occurs near living equivalent species of the Oak woodland and Chaparral Components. In the central Sierra Nevada both *Castanopsis* and *Chamaebatia* occur with related living members of the Border-redwood Component, which has a prominent place in the canyons in the central and northern parts of the range.

The 9 modern equivalent Mulholland species not indigenous to California all occur in areas with summer precipitation. These include representatives of the Oak woodland and Rocky Mountain Components of the Southwest American and West American Elements respectively, and of the East American and East Asian Elements. Representatives of the Oak woodland and Rocky Mountain Components in the southwestern United States show an ecological relationship much like that discussed above for the Oak woodland and Sierra-Cascade Components in California, and both are bordered by equivalents of the Chaparral Component. *Sapindus drummondii* and *Quercus vaseyana* are modern representatives of common Mulholland species no longer represented in California. Sixteen other modern equivalent Mulholland species range from California into the southwestern United States as identical or closely related plants, and are often associated with them. Equivalents of the Oak woodland

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Component include *Celtis reticulata, Quercus emoryi* (*wislizenii*),[2] *Quercus utahensis* (*lobata*), *Platanus wrightii* (*racemosa*), *Populus arizonica* (*fremontii*), *Prunus fasciculata,* and *Salix lasiolepis.* Representatives of the Chaparral Component found near at hand are *Cercocarpus betuloides, Dendromecon rigida, Fremontia mexicana* (*californica*), *Mahonia fremontii, Rhamnus ursina* (*californica*), *Rhamnus ilicifolia* (*crocea*), and *Rhus ovata.* These plants have a vertical distribution which includes Lower Sonoran and Arid Transition habitats, but they live regularly in the Upper Sonoran zone. In areas of high relief in this zone they are found with such representatives of the Rocky Mountain Component as *Acer grandidentatum* and *Populus acuminata,* both of which have equivalents in the Mulholland flora. Additional associates of this group include *Amelanchier, Prunus,* and *Fraxinus,* which also have identical or related species in California and fossil representatives in the flora.

Five Mulholland species, *Berchemia multinervis, Nyssa elaenoides, Populus washoensis, Quercus bockéei,* and *Q. simulata,* are members of the East Asian and East American Elements that characterized the Arcto-Tertiary Flora in western North America during the Miocene. These species, which are interpreted as relicts at Mulholland, find their nearest equivalents on the eastern sides of the northern continents, where rainfall is distributed rather evenly throughout the year, and where temperatures are moderate. *Acer bolanderi* of the Rocky Mountain Component shows suggestive relationships to the living eastern North American species *A. floridanum* Pax and *A. leucoderme* Small. All these modern species are hardly more than varieties of the widely distributed *A. saccharum* Marsh of eastern North America. *Acer grandidentatum* represents the most arid form of this group and, in view of the semiarid character of the Mulholland flora, might therefore be expected to compare somewhat more closely with *A. bolanderi.* In this connection it is significant that *Nyssa elaenoides, Populus washoensis,* and *Quercus simulata* have smaller leaves than their nearest Miocene relatives, resembling those found today on their closest representatives in the drier parts of their distribution.

These relationships of the Mulholland flora to modern vegetation suggest that three major plant communities contributed to the Mulholland sediments: (1) an oak savanna-woodland and its arid associates, (2) chaparral, and (3) a relatively mesic forest which may be termed a border-redwood forest. The relative abundance of the fossil species provides an index to their distribution about the Mulholland basin. Because the flora lived in a region of varied relief, physical conditions were diverse. Two extremes, the semiarid lowland association and the relatively mesic forest, will be discussed in this connection.

The dominants of the flora, including the species of *Quercus, Populus, Platanus, Sapindus,* and *Salix,* are considered to have lived at the immediate site of deposition. The abundance of oaks in the flora, together with the prevalence of grass remains, suggests savanna conditions in the immediate basin. This is consistent

[2] Species in parentheses are Californian equivalents of Mulholland fossils. These seem more nearly related to the fossils than the species cited, but the latter are nevertheless generally similar.

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with the occurrence of such grazing mammals as horses (*Nannippus, Pliohippus*) and camel (Camelidae) in the associated deposits (Stirton, 1939*a*). Over the cooler slopes the oaks presumably formed a woodland, much as their modern counterparts do. The associates of this semiarid savanna-woodland included *Celtis, Prunus,* and *Rhus,* as well as certain shrubs from the chaparral, and all of them probably occupied drier slopes, flats, and washes in exposed parts of the Mulholland basin.

Only a part of this dominant group has equivalent species at the fossil locality today. *Quercus lobata* is distributed widely over the area in a savanna habitat, and together with the willow, *Salix lasiolepis,* still contributes leaves and other structures to the stream at the fossil locality. *Populus fremontii, Platanus racemosa,* and *Quercus wislizenii* approach the abundance suggested by their Pliocene equivalents only in more interior localities, as at Mount Diablo, 15 miles distant, where precipitation is lower and extremes of temperature are greater. *Quercus vaseyana* ranges from western Texas into Mexico, in a region of biseasonal rainfall, and *Sapindus* is distributed throughout the southwestern United States and adjacent Mexico. When these are considered together with the 8 species having modern equivalents in southern California, there seems to be definite evidence of a drier and warmer climate than that now prevailing at the fossil locality. It is to be noted also that the modern flora of the region includes such species as *Acer macrophyllum, Alnus rhombifolia, Arbutus menziesii, Quercus kelloggii,* and *Umbellularia californica.* Of these only *Alnus, Arbutus,* and *Umbellularia* have representatives in the Mulholland flora. Their small numbers indicate that they were limited to more mesic habitats away from the immediate depositional area during Mulholland time.

The annual rainfall at the fossil locality today is somewhat higher than at Walnut Creek, 4½ miles northeast, where precipitation totals 17 inches. On the basis of a slightly higher elevation and a considerably more mesic flora, it is believed that the present rainfall at the fossil locality totals at least 22 or 23 inches yearly. By contrast, the dominants of the arid community in the Mulholland flora suggest that annual precipitation in the drier parts of the basin probably was in the neighborhood of 15 to 17 inches. It may be concluded that rainfall during Mulholland time was approximately 5 to 7 inches below that occurring at the fossil locality today, a conclusion implied by Dorf (1930). The present distribution of many of the equivalent Mulholland species to the south suggests that winter temperatures during the Pliocene were higher than those prevailing in the region today. The present difference between the temperature at the fossil locality and that of southern California is approximately 2° or 3° F. during the coldest months of the year. An even greater temperature difference may be noted by comparison with the southwestern United States, where other modern equivalents of the Mulholland species occur.

Chaparral is represented in the fossil flora by 11 species. Most of these are known from only a few or a moderate number of specimens, but they nevertheless form a more prominent component of the flora than the Border-redwood. Their poor quantitative representation probably is to be attributed to the occur-

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rence of this association on hill slopes bordering areas of accumulating sediments, rather than to its poor development as a community. Chaparral was of more diverse composition in central California during the Middle Pliocene than today. Since the climate in west-central California during this stage was drier and warmer, there is reason to assume that chaparral may have formed a more important community than it does at present. Such an interpretation is not inconsistent with the abundance of grass and oak in the flora, for their dominance suggests savanna-woodland areas over the lowlands about the immediate basin of plant accumulation. The chaparral community may well have been limited to slopes bordering the basin of deposition above the savanna, much as it is today throughout the south Coast Ranges and in a large part of southern California.

A relatively mesic forest in the Mulholland area was made up of members of the Border-redwood, Sierra-Cascade, and Rocky Mountain Components of the West American Element, and here also were the relicts of the East Asian and East American Elements. Although 19 plants are included, they comprise a small part of the Mulholland flora, for none is represented by more than a few specimens. The poor numerical representation of this group suggests that it was situated at some distance from the fossil locality, probably in Las Trampas Hills, directly to the southeast. This inference is consistent with the source of the sediments, for Miocene Briones fossils derived from the Las Trampas area occur as secondary deposits stratigraphically above and below the flora (K. A. Richey, oral communication, June 1938). Situated in this hilly region directly southeast of the fossil locality, these more mesic plants would be expected to extend their ranges to lower altitudes in cool canyons and on north slopes, where they would be in a position to contribute occasional leaves and seeds to sediments accumulating in the lower oak country.

The species of this group suggest local physical conditions considerably different from those prevailing at the immediate site of deposition, where *Platanus paucidentata, Populus prefremontii, Quercus wislizenoides, Sapindus oklahomensis,* and other Madro-Tertiary plants were abundant, as judged from their dominance as fossils. In order to determine the conditions under which this border-redwood forest lived, it is essential to distinguish between a marginal flora within the redwood belt and one at its southern end (Dorf, 1930, pp. 38–39). In the former the border character is due primarily to local topographic features, whereas in the latter it is controlled by climate. The extraordinary development of semiarid types in the Mulholland flora points to conditions such as prevail in southern and interior localities, rather than in northern and coastal. Judging from climatic data presented by Cooper for the broad-sclerophyll vegetation of California (1922), and from discussions by LaMotte (1936) and Dorf (1936) of essentially similar forest communities of late Tertiary age, the border-redwood forest and its associates lived under an annual rainfall of from 23 to 25 inches.

Certain plants in the flora suggest that there was summer precipitation. Three of the genera, *Berchemia, Nyssa,* and *Sapindus,* live today only in areas with

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summer rainfall, and the equivalent Miocene species are generally considered to have lived under a climate similar in this respect. Six additional species in the flora, *Acer bolanderi, Populus parce-dentata, P. washoensis, Quercus bockéei, Q. orindensis,* and *Q. simulata,* have their nearest modern correlatives in regions with summer precipitation. Although summer rainfall during Mulholland time was lower than in the Miocene, it was nevertheless sufficient for the persistence of the more hardy genera and species. As a result of the increasing continentality in post-Miocene time, it seems probable that Mulholland precipitation was distributed chiefly during two periods, as summer showers and winter rains.

Summarizing the evidence with respect to physical conditions in the Mulholland region, the following suggestions may be made:

1. The Mulholland flora lived on the leeward slopes of a low range corresponding in general position to the present Oakland-Berkeley Hills. The sediments in which the flora was preserved represent lacustrine and fluviatile deposits derived from Las Trampas Hills to the southeast.

2. Oaks formed savanna about the site of deposition, and their associates included plants whose nearest relatives now survive in the San Francisco Bay region, southern California, and the southwestern United States. Woodland and chaparral covered parts of the adjacent hills, and at higher elevations and on cooler slopes at lower altitudes a border-redwood forest attained limited growth. This included some of the more hardy members of the East American and East Asian Elements, and two species with living equivalents from the Rocky Mountains.

3. The climate at the fossil locality was both drier and warmer than at present. Annual rainfall, which varied from 15 or 17 inches in the oak savanna of the lowlands to approximately 23 or 25 inches in the border-redwood forest, was distributed in summer as well as in winter. Winter temperatures appear to have been somewhat higher than those now prevailing at the fossil locality.

Floristic Changes Following Mulholland Time and Their Bearing on the Development of Certain Plant Regions in the Western United States

In the preceding discussion of the modern relationships and physical conditions suggested by the Mulholland flora, it has been pointed out that this assemblage contains plants whose nearest relatives now occur in widely separated regions. In addition to the species related to plants now in eastern North America and northeastern Asia, there are others whose nearest relatives characterize certain plant regions in the western United States. Some of these, such as *Lyonothamnus floribundus* and *Quercus tomentella,* now make up a part of the insular flora of southern California, and others, for example *Ceanothus spinosus* and *Rhus laurina,* are common in coastal southern California. Two of the Mulholland living equivalents, *Castanopsis sempervirens* and *Chamaebatia foliolosa,* characterize the Sierra Nevada Transition forest, and two others, *Acer grandidentatum* and *Populus acuminata,* are typical of the Rocky Mountain area. The Mulholland species whose nearest relatives characterize these

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three regions (Sierra Nevada, southern California, Rocky Mountains) will now be considered from the standpoint of changing physical conditions in central California during later Cenozoic time. Such an analysis affords data relative to the differentiation of these plant regions, but the following discussion is considered only as an initial step toward a final interpretation.

Differentiation of the Southern and Central California Floras

The following living relatives of Mulholland species occur in southern California:

Ceanothus spinosus	Prunus fasciculata
Celtis reticulata	Quercus tomentella
Lyonothamnus floribundus	Rhus laurina
Mahonia fremontii	Rhus ovata

As noted above, two of these, *Lyonothamnus floribundus* and *Quercus tomentella,* are insular in distribution, *Ceanothus spinosus* and *Rhus laurina* are primarily coastal, and the remainder are typical of the interior. The writer has already pointed out that ancestors of these semiarid species were largely eliminated from central California in the later Pliocene, when conditions were becoming cooler and more moist (Axelrod, 1938, 1939). It must be noted, however, that four of these plants which occur typically in southern California have relict northern outposts in central California. *Rhus laurina,* a coastal species distributed from Santa Barbara southward, has been collected by the writer in the hills near Cayucos, 100 miles farther north. *Ceanothus spinosus* has a somewhat similar distribution. Characteristic of the coastal chaparral from the Santa Ynez Mountains southward, it occurs also in the southern Santa Lucia Mountains east of Cayucos. *Celtis reticulata* has an isolated occurrence near the town of Caliente in the southern Great Valley of California. Known from only a few localities in southern and southeastern California, hackberry attains optimum development in the southwestern United States. Another typical desert species, *Prunus fasciculata,* is represented by the variety *punctata* in the south Coast Ranges east of San Luis Obispo. Although pinyon pine (*Pinus monophylla* Torrey and Fremont) is not represented in the Mulholland flora, its fossil equivalent, *Pinus kelloggii* Webber, has been identified by L. H. Daugherty in the slightly younger Pinole tuff 20 miles north (oral communication, September 1937). Widely distributed throughout the arid interior parts of the western United States, pinyon pine ranges also into the San Rafael Mountains in the south Coast Ranges, as well as onto the western slopes of the southern Sierra Nevada in Kern County, 200 miles southeast of the Pinole locality.

Additional plants belonging to this group, but not represented by fossil equivalents in the Mulholland flora, are listed in table 13. All but 5 of these, *Adenostoma, Isomeris, Larrea, Stenotopsis,* and *Yucca,* have been recorded in Miocene and Pliocene floras elsewhere in California. It is believed that all of them, in addition to the 5 plants discussed above, may be interpreted as relicts of the early Pliocene invasion of west-central California by the Madro-Tertiary

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TABLE 13

MODERN SPECIES INTERPRETED AS RELICTS OF THE EARLY PLIOCENE INVASION OF CENTRAL CALIFORNIA BY THE MADRO-TERTIARY FLORA

Species	*Relict northern occurrences*	*Typical distribution*
Adenostoma sparsiflorum Hooker and Arnott	South Coast Ranges	Desert border
Arctostaphylos glauca Lindley	Mt. Diablo; Santa Cruz Mts.	Southern California
Arctostaphylos pungens H. B. K.	Mt. Hamilton Range (Pinnacles)	Southern California to Mexico
Ceanothus leucodermis Greene	Mt. Hamilton; Wawona	Southern California
Cercocarpus ledifolius Nuttall	Cobblestone Mt.; Tejon Quadrangle; inner north Coast Ranges	Mountain slopes of Great Basin and border areas
Forestiera neo-mexicana Gray	Mt. Diablo; Mt. Hamilton	Desert
Isomeris arborea Nuttall	Caliente Creek	Desert
Larrea mexicana Moricand	Upper San Joaquin Valley	Desert
Lepidospartum squamatum Gray	Salinas River	Desert
Prosopis juliflora DeCandolle	West of Bakersfield	Desert
Quercus palmeri Engelmann	West of Paso Robles	San Jacinto Mts. to Arizona and Mexico
Stenotopsis linearifolia Rydberg	South Coast Ranges	Desert
Yucca whipplei Torrey	Santa Lucia Mts.	Desert

Flora (Axelrod, 1939, pp. 49–58). Their distribution suggests that although a part of the Southwest American Element was eliminated in late Pliocene time, certain woody plants of southern derivation were able to persist in compensatory sites in central California many miles north of their normal ranges as established today. There are numerous herbaceous plants having a similar distribution (Hoover, 1937) that probably is to be interpreted in the same manner. Ancestors of modern southern California species had a large representation in the Middle Pliocene floras of central California, but they were greatly reduced here by the early Upper Pliocene (Sonoma flora). Judging from their rarity at this time, it would appear that the fundamental differences between the modern floras of central and southern California were inaugurated during the latter part of this stage. The occurrence of a characteristic fruit of *Juglans californica* Watson in the Pleistocene of the San Joaquin Valley (H. L. Mason, oral communication, July 1940) suggests that segregation continued into the latest Cenozoic. That it is still not completed is shown by the above-mentioned relict northern outposts of southern California species in central California.

Many of the modern equivalents of Mulholland species now surviving in southern California are of interior occurrence, but *Lyonothamnus floribundus, Ceanothus spinosus, Quercus tomentella,* and *Rhus laurina* are primarily insular

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and coastal. A study of the Miocene and Pliocene distribution of their fossil equivalents suggests that they have become adapted to moderate coastal conditions since the late Pliocene. The insular oak, *Quercus tomentella,* first appears as the closely related *Q. declinata* in the Middle Miocene Tehachapi flora from the western Mohave Desert (Axelrod, 1939), together with *Lyonothamnus;* today both are strictly insular in distribution. The leaves of these Miocene species are smaller than those produced by their modern equivalents, and those of the Pliocene species are of intermediate size. This seems consistent with an adaptation to a more moderate maritime climate in the later Tertiary, and agrees also with floristic evidence suggesting their segregation to a cooler coastal region (Axelrod, 1939, pp. 70–71). *Rhus laurina* is limited primarily to coastal southern California, but southward it occurs in the desert of northern Baja California (Shreve, 1936). It should be noted that during the Middle Pliocene in interior southern California, *Rhus prelaurina* lived in close proximity to desert-border conditions (Axelrod, 1937, p. 150). Furthermore, this species has been collected recently in the Mint Canyon flora of southern California (Axelrod, 1940*c*), where it is associated with desert-border vegetation.

These plants of Middle Tertiary north Mexican origin apparently have been restricted coastward since early Pliocene time. Simultaneously there must have been development of tolerance which has resulted in their becoming adapted to a climate with winter precipitation and a more moderate annual range of temperature. In both the insular species there has been visible morphological change, involving an increase in leaf size. This contrasts with the opposite trend to reduced leaf size commonly shown by species of northern origin (Chaney, 1938*b,* p. 393). In the latter case species have become adapted to arid climate, whereas the species of north Mexican origin have moved coastward to more mesic conditions.

This coastward restriction of species formerly having interior distribution has played a fundamental role in the segregation of the present southern California flora into its two major subdistricts, the coastal and interior (Abrams, 1910; Howell, 1929). Several typical coastal species range into the interior along river valleys with moderating summer fogs and ocean breezes; such relicts include *Juglans californica, Rhus laurina,* and *R. integrifolia.* All these have equivalent fossil species in the Middle Pliocene Mount Eden flora near the border of the Colorado Desert 40 miles inland from their nearest modern occurrences (Axelrod, 1937; 1939, p. 117). Coastward segregation of ancestors of these species and the insular endemics of north Mexican origin, in addition to many other typically coastal species as yet unrecorded in the Pliocene of interior southern California, is considered to have taken place in the late Pliocene and Pleistocene, when the Santa Ana Mountains and Puente Hills were uplifted at the west, and a hotter and drier climate developed over the inland area.

Differentiation of the Sierra-Cascade and Coast Redwood Forests

Attention has been directed to the fact that two typical members of the Sierran Transition forest, *Chamaebatia foliolosa* and *Castanopsis sempervirens,* are rep-

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resented by equivalent species in the Mulholland flora. In addition, Dorf has recorded 4 typical Sierran species, represented by the modern *Ceanothus integerrimus, Libocedrus decurrens, Pinus lambertiana,* and *Ribes nevadense,* which were associated with the coast redwood in the late Pliocene Santa Clara flora (1930, pp. 52–55). They occur today in the higher mountains of the inner Coast Ranges or above the redwood forest along the coast. Other characteristic members of the Sierran forest in similar situations in the Coast Ranges include such common species as *Abies concolor* and *Pinus ponderosa.* Although fossil representatives of Sierran species were associated with the redwood forest in Miocene and Pliocene times, their modern equivalent species do not occur in this forest today. Mason has suggested that the redwood and Sierran forests probably have become distinct only since later Pliocene time (1936, p. 188). They appear to have been segregated or selected on the basis of relative humidity, the redwood being limited to the coast, and the Sierran forest persisting in the interior and at higher elevations near the coast.

Recent studies have shown that in the Sierra Nevada there are Mio-Pliocene records of coast redwood associated with typical Sierran species and with the East American and East Asian Elements, as shown by Condit in chapter 2 of this volume. Besides *Sequoia langsdorfii,* whose nearest modern descendant is the coast redwood (*S. sempervirens*), transitional Mio-Pliocene floras in the central Sierra Nevada at middle elevations contain species of *Arbutus, Cornus, Philadelphus,* and *Umbellularia,* all of which have survived down to the present in modified form in the Sierra Nevada and make up an integral part of the Sierran Transition forest; other genera in these floras, such as *Berchemia, Carya, Liquidambar, Magnolia,* and *Ulmus,* are now extinct in the Pacific states.

Sequoia langsdorfii and many of its Miocene associates were greatly restricted in the Sierra Nevada during Lower Pliocene time. At this time, coast redwood may have survived in more northern parts of the range, at higher elevations where conditions were more moderate. Presumably the East American and East Asian Elements persisted in the Sierra Nevada for a longer time than the more sensitive coast redwood. Although *Sequoia langsdorfii* has not survived down to the present in the Sierra Nevada, many of its associates have persisted in modified form in canyons in the northern and central parts of the range. Among these are the following which occur today in the coast redwood forest, and are represented also by equivalent species associated with redwood in the Miocene to the north:

Acer macrophyllum
Alnus rhombifolia
Arbutus menziesii
Cornus nuttallii
Corylus californica
Fraxinus oregona
Lithocarpus densiflora
Philadelphus lewisii
Populus trichocarpa
Prunus demissa
Prunus emarginata
Pseudotsuga taxifolia
Quercus kelloggii
Rhus diversiloba
Taxus brevifolia
Torreya californica
Umbellularia californica
Woodwardia radicans

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As might be expected, canyons where these plants live in close association have the aspect of a redwood forest, but the coast redwood is absent owing to low winter temperatures and high evaporation in summer. Besides these trees and shrubs which still have a distribution in both forests, there are certain plants, such as *Acer circinatum* and *Castanopsis chrysophylla,* which occur typically with coast redwood in the north Coast Ranges, but are known only from isolated localities on the central and northern Sierra Nevada.[3] These are presumably relicts of the forest which occupied the region during the Middle Tertiary.

In connection with redwood in the Sierra Nevada, it should be noted that *Sequoia gigantea* now forms an integral part of the Arid Transition forest in the central and southern Sierra Nevada. *Sequoia* of the *gigantea* type has not been recorded in the Miocene of the Columbia Plateau and northern Great Basin, but the writer has recently collected a close relative of *S. gigantea* in the Upper Miocene at Coal Valley, western Nevada, 15 miles west of Hawthorne. Here it occurs with typical members of the northern Miocene forest (*Abies, Amelanchier, Cebatha, Mahonia, Pinus, Populus, Symphoricarpos, Trapa, Zelkova*) and a few of the Southwest American Element (*Celtis, Lyonothamnus, Quercus*). Judging from the character of this flora, it would appear that the ancestor of *S. gigantea* already had become adapted to an Arid Transition habitat by Upper Miocene time in the central Great Basin. It may be suggested that its apparent absence from the Miocene floras of the Columbia Plateau and northern Great Basin is due to its restriction to drier slopes above sites of deposition. Similarly, the Sierra redwood may not have been represented at middle elevations on the windward slopes of the central Sierra Nevada until Pliocene time, because climatic conditions during the Miocene were not sufficiently arid in that region.

It is not known definitely during which epoch the Arcto-Tertiary Flora invaded the Coast Ranges. Judging from the character of the Oligocene Weaverville (MacGinitie, 1937) and Lower Cedarville floras of northern California, and the Miocene floras of northwestern Nevada (LaMotte, 1936) and eastern Oregon (Chaney, 1938*b*), there is every reason to assume that this forest had occupied the higher parts of the north Coast Ranges by Miocene time. The later Tertiary history of *Sequoia* in this region differs from that in the Sierra Nevada in two important respects. In the first place, coast redwood has survived down to the present in the Coast Ranges, whereas it disappeared, or at least was greatly reduced, in the Sierra Nevada during early Pliocene time. Secondly, members of the East Asian and East American Elements survived longer in the Coast Ranges than in the Sierra Nevada. Such genera as *Castanea, Ulmus,* and *Trapa* are recorded with redwood near the coast in the Sonoma flora of early Upper Pliocene age; this flora is discussed in chapter 7 of the present volume. Genera representing these elements were greatly reduced in the Sierra Nevada by early Pliocene time. In other words, whereas coast redwood and members of the East Asian and East American Elements were largely

[3] *Acer circinatum* was collected in the central Sierra Nevada by H. L. Mason during the summer of 1940 (oral communication, September 1940).

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eliminated from the lower slopes of the Sierra Nevada by the early Pliocene, they were closely associated with members of the Sierran forest in the more humid coastal region into later Pliocene time. Differentiation of the Sierra-Cascade forest from the Arcto-Tertiary Flora thus took place earlier in the interior than in coastal regions.

Rocky Mountain Component in California

The occurrence of plants in the Mulholland flora whose nearest modern representatives are now characteristic of the Rocky Mountain region merits special attention. *Populus acuminata,* whose fossil equivalent is *P. parce-dentata,* ranges from British Columbia southward to the Mexican border in Arizona and New Mexico, and westward into Nevada. In addition to its Mulholland occurrence, *P. parce-dentata* has been recorded in the Lower Pliocene Diablo flora near Mount Diablo and in the Oakdale flora of the central Sierran foothill region. One other Mulholland species with Rocky Mountain affinities is *Acer bolanderi,* which closely resembles *A. grandidentatum.* The modern species ranges discontinuously from Montana southward into northern Mexico. The fossil species also occurs at Table Mountain and has been collected recently in the Mint Canyon flora of southern California.

The occurrence of ancestors of typical Rocky Mountain trees in California in late Tertiary time recalls the fact that there are a large number of species in California that are known also from the Rocky Mountain province. Long lists of these plants have been presented by Coville (1893), Piper (1906), and Munz (1935). Among the more notable trees in California which attain characteristic development in the Rocky Mountain province are (1) *Populus angustifolia* James, which grows along the South Fork of the Santa Ana River at an elevation of 6300 to 6500 feet in the San Bernardino Mountains, and on the desert slopes of that range in Rattlesnake Canyon at an altitude of 5500 feet; and (2) *Pinus flexilis* James, which grows in the San Bernardino and San Jacinto mountains of southern California, Mount Piños, and the southern Sierra Nevada. In addition, *Arctostaphylos parryana* Lemmon var. *pinetorum* (Rollins) Wieslander and Schreiber of southern California is found in Utah (Uinta Mountains) and Colorado (Uncompahgre Plateau); *Pinus monophylla* Torrey and Fremont of the Rocky Mountains and Great Basin occurs in the inner south Coast Ranges of California; *Cercocarpus ledifolius* Nuttall of the Great Basin and Rocky Mountain area occurs on the crest of Cobblestone Mountain in central Ventura County, and in the inner north Coast Ranges. When these species are considered together with the woodland and montane associations, as well as the numerous herbaceous plants common to the two regions, there seems to be little doubt of the historical relationship between the floras of the Rocky Mountains and California.

Available paleobotanical data suggest that the relationships have arisen through former east-west and north-south connections, depending on the particular elements under consideration, latitude, and geologic time. During the Miocene there were two generalized types of vegetation in the western United

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States: a mesic temperate forest, the Arcto-Tertiary Flora, extending from central California northward into Washington and eastward into the Rocky Mountains (Chaney, 1936*b*), and a semiarid woodland, the Madro-Tertiary Flora, at the south (Axelrod, 1939). These floras, which ultimately gave rise to the modern montane and woodland associations of the western United States (Axelrod, 1940*b*, pp. 482–484), persisted in the Great Basin area into early Pliocene time. Thus from a paleobotanical standpoint the intermediate mountainous areas of the Great Basin now supporting montane and woodland associations may be regarded as refugia of later Tertiary vegetation. Members of the montane flora in the higher Basin Ranges, such as the Charleston, White, and Toyabe mountains of Nevada, and the Uinta and Wasatch of Utah, are interpreted as survivors of the northern forest which extended southward during the middle and later Tertiary. Likewise the presence of typical Rocky Mountain montane species in southern California seems attributable to a southward extension of the northern forest along the Sierra Nevada and into southern California during the later Tertiary. But the occurrence of woodland plants common to California and the Rocky Mountain province is to be related to the Madro-Tertiary Flora which extended from southern California eastward through southern Nevada, Utah, and Colorado into the High Plains and southward into northern Mexico during the Miocene (Axelrod, 1939, map on p. 59). With the gradual development of desert conditions across the Great Basin province in the later Tertiary (Axelrod, 1940*b*), the woodland and montane vegetation was restricted gradually into the bordering mountains, where it has survived down to the present in modified form.

The Mulholland species with Rocky Mountain affinities, *Acer bolanderi* and *Populus parce-dentata,* although originally of northern origin from a generic standpoint, may have developed their modern characters at the south and thence spread northward during the middle and later Tertiary. This interpretation is suggested by the fact that they are comparatively rare or absent in the northern Miocene floras. If these plants had formed a regular part of the Arcto-Tertiary Flora, they would be expected to have a greater representation at the north. By contrast, they are known in more southerly floras, the Mulholland, Table Mountain, Mint Canyon, and Creede, and in all cases they are associated with the Southwest American Element. Members of the Rocky Mountain Component no longer indigenous to California are considered to have disappeared from this region in the later Pliocene as summer rains were eliminated.

Age of the Flora

The Pliocene age of the beds containing the Mulholland flora has previously been determined from their stratigraphic relations and associated plant, vertebrate, and invertebrate remains (Lawson, 1915; Dorf, 1930; Stirton, 1939*a*). On the basis of rather limited plant material, Dorf placed the flora at the base of the Middle Pliocene (1930, p. 6). The present collection is sufficiently large to permit a detailed age analysis of the flora, and to indicate more definitely that its position within the Pliocene is approximately where Dorf placed it.

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Later Tertiary floras are provincial in character as compared with those from older horizons. Evidence recently gathered points to the conclusion that floristic succession, though following the same general course over much of the western United States at middle latitudes, differed with respect to the time of appearance of new and disappearance of older elements in the various provinces (Axelrod, 1940*b*, pp. 484–486). Thus by taking into account its geographic position and considering the character of its floristic elements and components, the approximate age of the Mulholland flora may be determined.

The Border-redwood Component had a more limited distribution in California during the Middle Pliocene than later in the epoch. Middle Pliocene floras of central California containing members of this community all suggest conditions comparable with those now found along the southern and interior borders of the forest in the south Coast Ranges. The abundance of xeric oaks in the Mulholland flora suggests a similar aspect for the assemblage, and thus points to its Middle, rather than Upper, Pliocene age. The poor representation of such plants as *Alnus merriami, Arbutus matthesii,* and *Umbellularia salicifolia* in the flora is consistent with such an age assignment. Since their nearest equivalent species are common at the fossil locality today, they may be assumed to have extended their ranges into the immediate area only in the later Pliocene, when the climate was becoming cooler and more moist.

The East American and East Asian Elements are commonly associated with the Miocene forest at middle latitudes (Chaney, 1936*b*). *Berchemia multinervis, Populus washoensis,* and *Nyssa elaenoides* of the former, and *Quercus bockéei* and *Q. simulata* of the latter, appear in the Mulholland flora. It is to be emphasized that although these species occur in the flora, they form the rarest group in it, in contrast with their dominance in the Miocene floras. Since the mid-Lower Pliocene Black Hawk Ranch flora on the southwestern slopes of Mount Diablo 12 miles distant is characterized by more numerous members of this group (chap. 4 above), it would appear that the Mulholland is considerably younger, that is, of Middle Pliocene age.

The Southwest American Element forms the dominant part of the Mulholland flora. This group of plants, along with many others, developed in northern Mexico and the southwestern United States in the Middle Tertiary (Axelrod, 1939). Spreading northward as conditions became drier in the later Miocene, these plants gradually displaced a large part of the Arcto-Tertiary Flora in central California. *Lyonothamnus* has persisted in scarcely modified form as an insular endemic genus of southern California. Other modern Mulholland equivalents, for example *Celtis reticulata, Fremontia californica, Quercus chrysolepis,* and *Rhus ovata,* still occur in southern California and in the southwestern United States, forming a wide-ranging group. A few, such as *Populus fremontii, Platanus racemosa,* and *Quercus engelmannii,* are represented by phylads across the desert region, and certain members of the element no longer survive in California.

Plants of this latter group include *Mahonia marginata, Quercus orindensis,* and *Sapindus oklahomensis.* It may be noted here that the species recorded

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tentatively as *Berchemia multinervis* may possibly represent the genus *Karwinskia,* in which case it would belong to the Southwest American rather than the East American Element. When these plants are considered together with the 8 species in the flora whose nearest modern representatives are now restricted to southern California, the evidence for the Middle Pliocene age of the flora appears conclusive. It seems certain that if the flora were of Lower Pliocene age, fewer Madro-Tertiary species would be represented, since members of the East American Element dominate the Black Hawk Ranch flora of that stage, as stated above. We should expect to find that at the close of Lower Pliocene time, with continued elevation of the Berkeley-Oakland Hills and the resultant desiccation of the interior region, these Miocene relicts were restricted to areas of their upland occurrence and thus enter the accumulating record as a minority group; furthermore, additional semiarid southern types would now invade lowland sites. The abundant representation of the latter, and the limited occurrence of the former, seem therefore to indicate the early Middle Pliocene age of the Mulholland flora.

The stratigraphic range of the 34 Mulholland species occurring as identical or closely related species in Oligocene, Miocene, and Pliocene floras in the western United States is shown in table 14. This table reveals several important features which find an explanation in the history and development of the northern and southern Middle Tertiary forests.

The Arcto-Tertiary Flora, as represented by the Oligocene and Miocene floras of the region from central California northward through the Great Basin and Columbia Plateau, has 9 identical species in common with the Mulholland, and the following which are related to Mulholland species:

Related Oligocene and Miocene species	*Mulholland species*
Amelanchier dignatus (Knowlton) Brown	A. sp. Dorf
Fraxinus sp. MacGinitie	F. caudata Dorf
Populus eotremuloides Knowlton	P. alexanderi Dorf
Quercus schofieldii Hollick	Q. bockéei Dorf

The Mulholland species listed above are derivatives of the northern Miocene plants, and differ from them in having leaves of smaller size and thicker texture. Further collections may show that two other Mulholland species, *Populus washoensis* and *Quercus simulata,* also belong in this category; they have not been designated as distinct from the Miocene species because they are represented by insufficient material. This reduction in leaf size has been ascribed to the general trend toward aridity in the western United States during the later Tertiary (Chaney, 1938*a*, pp. 212–213). The presence of small-leafed derivative Miocene species in the Mulholland suggests its post-Miocene age. In view of its coastal position, their occurrence at Mulholland can also be considered to indicate an age slightly younger than the mid-Lower Pliocene Black Hawk Ranch flora. Occurring in a near-by region, this flora includes species with larger leaves characteristic of the Miocene to the north (chap. 4 above, p. 93).

The Mulholland has more in common with the early Middle Miocene Teha-

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chapi flora of the Mohave Desert than with any other single Miocene flora in the western United States. Of the 34 Mulholland species with outside distribution, 12 occur in the Tehachapi, and 2 others, *Cercocarpus cuneatus* and *Mahonia marginata,* are closely related to the Tehachapi *C. antiquus* and *M. mohavensis;* both the Miocene and the Pliocene species have been referred to the same modern equivalents, and additional material may show that they are not distinct. The high correlation with the Tehachapi indicates that during later Miocene and early Pliocene times, the semiarid Tehachapi species were migrating northward and coastward into the Mulholland area. This trend is illustrated by the fact that these semiarid species have been recorded at geographically intermediate localities in late Miocene and early Pliocene times. They regularly appear in more northern areas as the Arcto-Tertiary Flora shows (*a*) a restriction of redwood, (*b*) decreasing numbers of East Asian and East American species, (*c*) the development of smaller and thicker-textured leaves by certain members of the forest, and (*d*) an increase in plants whose nearest relatives now occupy more exposed positions bordering the redwood forest and its related communities.

Sixteen of the Mulholland species have been recorded in floras transitional in age between the Miocene and Pliocene. Reference to table 14 will show that these include several typical Miocene species of northern origin, such as *Cornus ovalis, Populus washoensis, Quercus simulata,* and *Salix hesperia;* other Miocene species whose northern origin is less well established are *Arbutus matthesii, Castanopsis perplexa,* and *Umbellularia salicifolia.* An equal number of Mulholland species recorded also from the Mio-Pliocene, including such typical forms as *Celtis kansana, Platanus paucidentata,* and *Quercus wislizenoides,* are interpreted as southern in origin. The Mio-Pliocene floras most similar to the Mulholland are the Remington Hill and Table Mountain floras, each of which has been shown to include more Madro-Tertiary species than the Lower Idaho at the north, and the coastal Neroly flora.

Lower Pliocene floras in the western United States have 15 identical species in common with the Mulholland, and 2 closely related species. It may be noted that there is a closer relationship to the Esmeralda and Upper Truckee floras of the interior than to the Black Hawk Ranch flora 12 miles east of the Mulholland. This is due to the fact that the Black Hawk Ranch represents a relict Arcto-Tertiary forest which persisted under favorable coastal conditions into mid-Lower Pliocene time. Contemporaneous floras east of the Sierra Nevada are semiarid in aspect, have fewer members of the East American and East Asian Elements, have derivative Miocene species, and contain members of the Southwest American Element. Although members of this latter element had a restricted upland occurrence near Black Hawk Ranch, they did not dominate the lowlands of this region until late in the stage, when conditions became drier and warmer.

Eighteen Mulholland species are represented by identical plants in the Middle Pliocene floras of California. Two of these in central California, the Oakdale and Petaluma, account for 16 of them, and this number may be increased when

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TABLE 14

STRATIGRAPHIC DISTRIBUTION OF P

SPECIES (Total, 34)	OLIGO-MIOCENE	MIOCENE						
		MIDDLE AND UPPER						
	Bridge Creek	Salmon	Latah	Tehachapi	Succor Creek	Mascall	Trout Creek	Blue Mountains
Acer bolanderi	...	...	...	...	...	...	...	...
Alnus merriami	...	...	...	...	...	...	...	...
Amelanchier sp.	o	o	o	...	...	o	o	o
Arbutus matthesii	x	...	x	...	...	x	...	...
Berchemia multinervis	...	...	...	...	...	...	...	...
Castanopsis perplexa	...	...	x	...	x	x	...	x
Celtis kansana	...	...	...	x	...	...	...	...
Cercocarpus cuneatus	...	...	...	o	...	...	...	...
Chamaebatia prefoliolosa	...	x	...	...	...	...	...	...
Cornus ovalis	x	...	x	...	x	...	...	...
Fraxinus caudata	o	...	o	...	...	...	o	...
Fremontia lobata	...	...	...	x	...	...	...	...
Lyonothamnus mohavensis	...	...	...	x	...	...	...	...
Mahonia marginata	...	...	...	o	...	...	...	...
Nyssa elaenoides	...	...	...	...	...	...	...	...
Photinia sonomensis	...	...	...	x	...	...	...	...
Platanus paucidentata	...	...	...	x	...	...	...	...
Populus alexanderi	...	...	...	x	o	...	...	o
Populus parce-dentata	...	...	...	...	...	...	...	...
Populus prefremontii	...	...	...	x	...	...	...	...
Populus washoensis	...	...	...	...	x	...	...	x
Prunus moragensis	...	...	...	...	...	...	...	...
Prunus prefasciculata	...	...	...	x	...	...	...	...
Quercus bockéei	...	...	...	...	...	...	...	...
Quercus declinata	...	...	...	x	...	...	...	...
Quercus moragensis	...	...	...	...	...	...	...	...
Quercus simulata	o	...	x	...	x	x	x	x
Quercus wislizenoides	...	...	...	...	...	...	...	...
Rhamnus precalifornica	...	...	...	x	...	...	...	...
Rhus prelaurina	...	...	...	...	...	...	...	...
Salix hesperia	...	...	x	...	x	x	...	...
Salix wildcatensis	...	...	...	x	...	...	...	...
Sapindus oklahomensis	...	...	...	...	...	...	...	...
Umbellularia salicifolia	?	...	x	x	o	x	...	...
Identical species	2	1	6	12	5	5	1	3
Closely related species	3	1	2	2	2	1	2	2
Identical species in stage	3					18		
Closely related species in stage	3					3		
Identical species in epoch					19			
Closely related species in epoch					4			

x = identical species; o = closely related species.

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further collections are made. Thus the coastward movement of semiarid Oak woodland and Chaparral Components that characterized the Mulholland took place in mid-central California during late Lower and early Middle Pliocene time. As a reflection of the increased aridity in this region, members of the East Asian and East American Elements show a reduction in numbers, the Redwood Component is highly restricted in occurrence, members of the Border-redwood Component are abundant, and certain members of the Arcto-Tertiary Flora have leaves of smaller size and thicker texture than had their Miocene relatives in this region earlier in the epoch.

The two Upper Pliocene floras of coast-central California, the Sonoma and Santa Clara, have 12 species in common with the Mulholland. These are largely members of the Border-redwood Component, but there are a few members of the Oak woodland and Chaparral. Their reduction in these floras, as compared with their dominance in the Middle Pliocene, agrees with the fact that the climate was becoming cooler and more moist in the late Pliocene.

This discussion of the stratigraphic and geographic distribution of vegetation related to the Mulholland flora may be summarized as follows:

1. The Mulholland has 27 species represented by identical or closely related plants in the two major forests that characterized the western United States in late Oligocene and Miocene times: the Arcto-Tertiary Flora of the Columbia Plateau and adjacent areas, and the Madro-Tertiary Flora of southeastern California. Of these, 13 had an origin in the northern forest and 14 in the southern woodland.

2. Transitional Miocene and early Pliocene occurrences of plants most nearly related to Mulholland species are in localities geographically intermediate between Oregon and southern California. Floras in west-central California during these stages have an overwhelmingly Miocene aspect in consequence of their coastal location.

3. Middle Pliocene occurrences of Mulholland species are in central California and in coastal localities.

Associated Vertebrate Faunas

Pliocene vertebrate remains collected from two horizons near the fossil-plant localities lend considerable weight to the early Middle Pliocene age assignment of the Mulholland flora. One locality is situated 300 yards south and within a few feet stratigraphically of the plant-bearing horizons (U. C. loc. V3303). Stirton lists Antilocapridae, goose tracks, and proboscidean tracks from this locality (1939*a*, p. 366). A larger fauna occurs at Mulholland, site 2 (U. C. loc. V3611), a mile to the northwest and about 400 feet higher in the section. The following have been identified here: ?*Hypolagus*, Megalonychidae, Canidae, *Nannippus* sp., *Pliohippus* cf. *spectans*, *Teleoceras*, and Camelidae. Stirton considers that both of these horizons are of Middle Pliocene age (1939*a*, p. 366), and has indicated that they probably belong to the early part of that stage (oral communication, 1942).

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Summary

The Pliocene Mulholland flora of 43 species has been collected from continental sediments in the eastern Oakland-Berkeley Hills. The dominant association surrounding the Mulholland basin of deposition was an oak savanna, with many species whose nearest relatives now occur far to the south. At higher elevations several hardy Miocene relicts persisted in a border-redwood forest.

The suggested climate differed from that now prevailing at the immediate fossil locality in having a slightly lower annual rainfall, summer precipitation, and higher winter temperatures.

The following suggestions with respect to the development of certain plant regions in the western United States are made: (*a*) The vegetation of central and of southern California became distinct only in the latest Cenozoic. (*b*) Differentiation of the Sierra-Cascade and coast redwood forests from the generalized Arcto-Tertiary Flora that invaded both the Sierra Nevada and the Coast Ranges in the Middle Tertiary continued through most of the Pliocene. (*c*) The close relationship between the woodland and montane vegetation of California and that of the Rocky Mountains finds an explanation in related Miocene and Pliocene vegetation which extended across the intervening Great Basin province.

An analysis of the representation of the northern and southern floristic elements in the Mulholland flora points to its early Middle Pliocene age, an interpretation in harmony with stratigraphic and vertebrate evidence.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class ANGIOSPERMAE
Subclass MONOCOTYLEDONES
Family TYPHACEAE

Typha lesquereuxi Cockerell

Typha lesquereuxi Cockerell, Bull. Amer. Mus. Nat. Hist., vol. 24, p. 79, pl. 10, fig. 46, 1908.

Characteristic remains of cattail are abundant in the flora and suggest the presence of slow-moving water and small lakes in the region. This inference is consistent with the general character of the sediments, for ripple marks like those formed along the borders of lakes commonly occur in the sandstones and shales.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1596.

Family GRAMINEAE

Poacites sp.

Fragments of grass are abundant throughout the plant-bearing horizons, but are too fragmentary and lacking in diagnostic characters to be assigned to any modern genus. Their abundance in the flora, together with the dominance of oaks, clearly suggests open savanna conditions about the immediate basin, a conclusion in harmony with the occurrence of grazing mammals in the associated sediments.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1597.

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Subclass DICOTYLEDONES
Family SALICACEAE

Populus alexanderi Dorf

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, figs. 10, 11 (not fig. 9, which is *P. prefremontii* Dorf); pl. 7, figs. 2, 3 (not fig. 1, which is *P. prefremontii*), 1930.

Condit, Carnegie Inst. Wash. Pub. 553, p. 40, 1944 (see synonymy).

Chaney has emphasized the points of difference between this species and the Miocene *Populus eotremuloides* Knowlton (Chaney, 1938*a*, p. 215), which is related also to the modern black cottonwood of western North America, *P. trichocarpa* Torrey and Gray. *Populus emersoni* Condit (1938, p. 255) does not appear to be distinct from the Pliocene species.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1600.

Populus parce-dentata (Lesquereux) new combination

(Plate 27, figures 1, 3)

Betula parce-dentata Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 242, pl. 50, fig. 12, 1883.

Betula parce-dentata Lesquereux, originally assigned to a locality in the John Day Valley by Lesquereux, has been shown by Knowlton (1919, p. 116) to have come from a locality known as "South of Mount Diablo, California." The precise locality of this Lesquereux material is now known, according to J. C. Merriam, to be the Railroad Ranch locality near the Mount Diablo Country Club (U. C. loc. P3647). The plant-bearing strata at this locality are several hundred feet above the uppermost invertebrate horizons of the Neroly, and separated from the Neroly by a conglomerate. The lithology at this locality is identical with that of plant-bearing strata in the Diablo formation 2 miles farther south (see chap. 8, p. 213). Recent field work here by B. L. Clark and the writer shows conclusively that Lesquereux's "South of Mount Diablo" locality is in the lower part of the Diablo formation. The Diablo unconformably overlies the Mio-Pliocene Neroly and conformably underlies the mid-Lower Pliocene Black Hawk Ranch vertebrate fauna and flora.

Examination of the type specimen of *Betula parce-dentata,* which is in the paleobotanical collections at the University of California, shows conclusively that it is a cottonwood and that it is indistinguishable from leaves produced by the modern *Populus acuminata* Rydberg. Two additional leaves of similar character in the Mulholland flora, together with the original material, form the basis for the following description.

Description. Leaves ovate-lanceolate, acuminate above and acute to cuneate below; 4.0 to 4.7 cm. long and 2.8 to 3.4 cm. wide, greatest width in the lower ⅓ of the blade; only the base of a petiole preserved, medium; midrib firm; alternate secondaries relatively straight or at least only slightly curved, diverging normally at about 40° from the midrib, looping upward along the margin; basal secondaries sometimes of subprimary nature but mostly weakly developed; a thin marginal vein bordering the lower part of the blade to about the point of maximum width; conspicuous intersecondaries approaching the secondaries in strength; tertiaries poorly preserved, but apparently irregular; marginal teeth crenate-dentate and glandular, directed outward in the lower part of the blade and forward above; texture heavy.

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Discussion. There are two cottonwoods in the later Tertiary of the West which might be confused with *Populus parce-dentata.* In the first place, the Creede cottonwood which was originally described as *Alnus larseni* Knowlton (1923) may not be distinct from *P. parce-dentata.* However, not only are most of the Creede specimens in the collections at the University of California and at the U. S. National Museum consistently larger than *P. parce-dentata,* but the teeth on the Creede leaves are more numerous and more rounded. If additional material of *P. parce-dentata* shows that its characters include the Creede within its range of variation, the Creede species must then be placed in synonymy. Nevertheless, these species may well be distinct, for in later Tertiary time the *P. acuminata* group may very possibly have been represented in the western United States by a phylad comparable with the modern *Populus fremontii* plexus. In view of this possibility, and because there now seem to be differences between the California and Colorado specimens, it seems best only to point out here the relationships of both the California and the Colorado species to the modern *P. acuminata.*

The only other cottonwood in the later Tertiary of the western United States which might be confused with this species is *Populus alexanderi* Dorf. Its leaves are easily distinguished by the following characters: (*a*) the secondaries are relatively straight in *P. parce-dentata,* whereas they are commonly bowed in *P. alexanderi;* (*b*) in *P. parce-dentata* the base of the leaf is acute to cuneate, but in *P. alexanderi* it is more than acute and commonly rounded to subcordate; (*c*) the apex in *P. parce-dentata* is regularly acuminate, and it is mostly rounded to acute in *P. alexanderi;* (*d*) the basal secondaries are rarely well developed in *P. parce-dentata,* and they usually are strong in *P. alexanderi.*

All specimens of *Populus parce-dentata* closely resemble the leaves of the modern *P. acuminata* Rydberg. This is a typical Rocky Mountain species, ranging from Alberta to southern New Mexico and southeastern Arizona. In areas of its southern distribution many of its associates have equivalent species in the Mulholland flora. The present occurrence of *P. acuminata* on the eastern front of the Sierra Nevada in Inyo County, California, is probably a relict of the later Tertiary.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1598, 1599.

Populus prefremontii Dorf

(Plate 27, figures 2, 4; plate 28, figure 1)

Populus prefremontii Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 77–78, pl. 7, fig. 4, 1930. Condit, Carnegie Inst. Wash. Pub. 553, p. 41, pl. 4, fig. 6, 1944 (see synonymy).

Numerous well preserved specimens represent this species in the Mulholland. Common in the Pliocene of California, it has been recorded also in the Middle Miocene Tehachapi flora of the Mohave Desert, and in the Mint Canyon flora of southern California. Its affinities, both past and present, suggest that the modern species is a phylad of southern interior origin.

One of the figured specimens of *Populus prefremontii* (pl. 27, fig. 4), as well as others in the flora, differs from the typical leaves produced by that species and its nearest relative, *P. fremontii,* in having small teeth and a distinctly triangular outline. For the present these specimens are considered to represent *P. prefremontii* because leaves of this type are produced occasionally by the living *P. fremontii.* These occur most frequently in the drier parts of its distribution, and particularly in desert-

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border areas. As might be expected, such members of the *fremontii* group as *P. macdougalii* Rose and *P. wislizenii* Sargent, which at best seem to be only poorly defined varieties of *P. fremontii,* and are characteristic of desert regions, also produce leaves which resemble the fossils.

Populus dimorpha Brandegee of Sonora and Sinaloa has leaves which are superficially like the fossils, but they differ in the character of the secondary venation in the upper part of the blade. The secondaries in *P. dimorpha* extend upward toward the apex and are essentially parallel to the midrib, a character not present in the fossils.

These Mulholland leaves may represent a species of the *fremontii* group which has no close living relative. Until additional material can be obtained from other localities, they are retained as *P. prefremontii.* It is significant that a single leaf of this type is represented in the Mint Canyon flora of southern California, which has many species of desert-border character. Further collections here are expected to clear up the problem.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 330, 332; plesiotypes, nos. 1601, 1602, 1603.

Populus washoensis Brown

Populus washoensis Brown, Jour. Wash. Acad. Sci., vol. 27, p. 516, 1937 (see synonymy). Axelrod, Carnegie Inst. Wash. Pub. 553, p. 98, pl. 22, figs. 1, 2, 1944 (see synonymy).

A characteristic and well preserved leaf impression represents the Mulholland occurrence of this species. In addition to its northern Miocene records in the Upper Cedarville and Thorn Creek floras, it is now known from the Pliocene at Black Hawk Ranch, at Chalk Hills (Truckee), and in the San Joaquin formation.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1604.

Genus **SALIX** Linnaeus

Further collections from the Etchegoin and San Joaquin formations of the Coalinga district in the south Coast Ranges have shown that the large willow-like leaves recorded there as *Salix coalingensis* Dorf are in reality those of *Persea.* The new material obtained here shows a complete range in leaf size and shape from typical large *Persea* leaves to the more slender willow-like forms. Thus, these specimens of *Salix coalingensis* (Dorf, 1930, pl. 7, fig. 7; pl. 8, figs. 1, 2) are recorded as a new combination: *Persea coalingensis* (Dorf) Axelrod. The Tehachapi avocado, *Persea* sp. Axelrod (1939, pl. 8, fig. 3), is referable also to this species, and one of the specimens of *Fraxinus caudata* Dorf (1930, pl. 13, fig. 7) from the Coalinga region likewise represents the same species. One specimen of *F. caudata* from the Wildcat locality (*ibid.,* pl. 13, fig. 6) also represents avocado. As now restricted, the type of *F. caudata* is represented only by the specimen shown by Dorf on plate 13, figure 8.

In his description of *Salix coalingensis,* Dorf included as a cotype with this Coalinga material an undoubted willow leaf from the Mulholland locality (1930, pl. 7, fig. 6). Additional collections here have yielded material ranging from relatively small, slender leaves to larger specimens which differ in no way from *S. hesperia* (Knowlton) Condit. On this basis, the specimen figured by Dorf as *S. coalingensis* (pl. 7, fig. 6) is placed in synonymy with *S. hesperia,* which shows close relationship to the living *S. lasiandra* Bentham.

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One other specimen figured as *S. coalingensis* is also a willow (Dorf, 1930, pl. 7, fig. 5). This specimen from the Wildcat locality, which differs from the preceding species in having an entire margin, and in its heavier and more irregular secondaries and comparatively few intersecondaries, seems closely related to the modern *S. lasiolepis* Bentham. It is here given a new name, *Salix wildcatensis* Axelrod, for its original locality. Belonging in synonymy with this species are the specimens of *S. coalingensis* from the Mount Eden (Axelrod, 1937) and Tehachapi floras (Axelrod, 1939).

From the foregoing evidence, the following changes in taxonomy are proposed:

Persea coalingensis (Dorf) Axelrod, new combination

Salix coalingensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pl. 7, fig. 7; pl. 8, figs. 1, 2, 1930.

Fraxinus caudata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pl. 13, figs. 6, 7, 1930.

Persea sp. Axelrod, Carnegie Inst. Wash. Pub. 516, pl. 8, fig. 3, 1939.

Salix hesperia (Knowlton) Condit

Salix coalingensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pl. 7, fig. 6, 1930.

Salix wildcatensis Axelrod, new name

Salix coalingensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pl. 7, fig. 5, 1930.

Salix coalingensis Dorf. Axelrod, Carnegie Inst. Wash. Pub. 476, III, pl. 4, fig. 8, 1937.

Salix coalingensis Dorf. Axelrod, Carnegie Inst. Wash. Pub. 516, p. 90, 1939.

Salix hesperia (Knowlton) Condit

Salix hesperia (Knowlton) Condit, Carnegie Inst. Wash. Pub. 553, pp. 41–42, pl. 4, fig. 7, 1944 (see synonymy and discussion).

Salix coalingensis Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 78–79, pl. 7, fig. 6 only, 1930.

As noted above, this species differs from *Salix wildcatensis* in having numerous and thin looping secondaries and intersecondaries, and in having a serrulate margin. Whereas the leaves of *S. hesperia* are typically lanceolate and may have acuminate tips, apices of the leaves of *S. wildcatensis* are more typically blunt.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 336; nos. 1605, 1606.

Salix wildcatensis new name

Salix coalingensis Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 78–79, pl. 7, fig. 5 only, 1930.

Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 170–171, pl. 4, fig. 8, 1937. Carnegie Inst. Wash. Pub. 516, p. 90, 1939.

An abundance of specimens in the Mulholland flora shows this willow to be related to the modern *Salix lasiolepis* Bentham, a species now common at the fossil locality.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1607, 1608.

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Family BETULACEAE

Alnus merriami Dorf

(Plate 27, figure 6)

Alnus merriami Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 80–82, pl. 8, figs. 6, 7, 1930.

Two battered specimens, suggesting transport for some distance into the Mulholland basin, are referred to this Pliocene alder. *Alnus merriami* closely resembles the modern *A. rhombifolia* Nuttall, a common alder along the stream at the fossil locality today. The white alder is believed to have extended its range into the immediate vicinity of the fossil locality later in the Pliocene or during the Pleistocene, when the climate was cooler and moister than during Mulholland time.

In the writer's opinion there is considerable doubt as to whether this species is distinct from *Alnus corrallina* Lesquereux. According to the locality data accompanying them (Lesquereux, 1883, p. 243), the type specimens of *A. corrallina* are from Corral Hollow and Bridge Creek. Knowlton (1919, p. 63) subsequently pointed out that the specimen ascribed to Bridge Creek actually came from a locality known as "South of Mount Diablo, California." Examination of the types in the paleobotanical collections at the University of California shows that all specimens of *A. corrallina* figured by Lesquereux are from this locality. Likewise, the Lesquereux specimens figured by Condit (1938) from a supposed unknown locality in Corral Hollow are also from a locality labeled "South of Mount Diablo," as may be seen from data on the backs of the specimens. The stratigraphic position of this locality is discussed under *Populus parce-dentata* on page 129 of this chapter.

Alder leaves are especially abundant in the collections from the type locality of *A. corrallina,* a total of 87 having been counted in the Lesquereux material. Variation ranges from the type specimens, having rather numerous, closely spaced secondaries, to leaf impressions with fewer and wider-spaced secondaries which are identical with the material of *A. merriami* Dorf. Until additional specimens of *A. merriami* can be obtained so as to indicate more fully the taxonomic features of the species, it seems best only to point out its relationship to *A. corrallina.*

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1610; no. 1609.

Family FAGACEAE

Castanopsis perplexa (Knowlton) Brown

(Plate 31, figure 6)

Castanopsis perplexa (Knowlton) Brown, Jour. Wash. Acad. Sci., vol. 30, p. 348, 1940 (see synonymy and discussion).

Two characteristic leaves in the flora closely resemble those of the bush chinquapin, *Castanopsis sempervirens* Dudley. This modern species is now a characteristic member of the Sierra Nevada forest at upper-middle elevations, and ranges southward into southern California. Its probable significance in the Mulholland flora is discussed in detail on page 112.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1611; nos. 1612, 1685.

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Quercus bockéei Dorf

Quercus bockéei Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 84–86, pl. 9, figs. 1–3, 1930.
Condit, Carnegie Inst. Wash. Pub. 553, p. 76, pl. 15, fig. 2, 1944 (see synonymy).

In discussing the modern relationships of this oak, Dorf has indicated that it has affinities with certain Mexican species, notably *Quercus galeottii* Martens. *Quercus bockéei* differs fundamentally from *Q. galeottii* in that the secondaries in leaves of the modern species characteristically bifurcate along the margin, a character not shown by the fossil. A detailed comparison of *Q. bockéei* with all available American oaks, in addition to the other fagaceous genera, indicates that it does not have any close living counterpart in the North American flora. Greatest affinity has been noted with the Asiatic Fagaceae, particularly *Castanopsis, Quercus,* and *Cyclobalanopsis.* Until more herbarium material can be examined, the writer prefers to consider *Q. bockéei* a member of the East Asian Element, without making specific reference to any living counterpart.

Among described fossil oaks, *Q. bockéei,* although slightly smaller, does not seem to be distinct from *Quercus schofieldii* Hollick, which has been recorded from the St. Eugene silts of Miocene age in British Columbia.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1613.

Quercus declinata Dorf

Quercus declinata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 88–89, pl. 8, fig. 13 (not fig. 12, which is *Q. hannibali* Dorf), 1930. Carnegie Inst. Wash. Pub. 476, II, p. 114, pl. 2, fig. 2, 1936.
Axelrod, Carnegie Inst. Wash. Pub. 516, p. 97, pl. 7, figs. 12, 13, 1939.

Well preserved specimens showing both serrate and entire margins are clearly referable to this fossil equivalent of the modern *Quercus tomentella* Engelmann of insular southern California and Guadalupe Island. It is to be noted that over 15 of its modern associates on these islands have fossil equivalents in the Mulholland flora.

The fossil leaves average somewhat smaller than those produced by the modern species, but are definitely larger than those recorded from the interior Tehachapi and Idaho floras. A similar trend has been noted in two other insular species having equivalents in the fossil record, *Prunus lyonii* Sargent and *Lyonothamnus floribundus* Gray. This adaptation of species of southern interior origin to coastal conditions, involving increased leaf size during the later Tertiary, is in sharp contrast with the trend to smaller leaf size commonly encountered in species of northern origin.

One of the types of *Q. declinata* (Dorf, 1930, pl. 8, fig. 12) represents *Q. hannibali* Dorf; it differs from *Q. declinata* in its more numerous secondaries, in the character of the tertiaries, and in the teeth.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1614, 1615, 1616.

Quercus moragensis new species

(Plate 29, figures 1–3)

Description. Leaves pinnately parted into 3 or 4 lobes, the lobes commonly broadened toward the apex; lobes entire or with minor lobes; length 3.0 to 6.0 cm., width 2.0 to 3.5 cm.; base of leaf acute to cuneate; alternate secondaries diverging

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at angles of from 30° to 75°, but usually more or less constant for the individual leaves; becoming thin and wavering in the tips of the lobes; irregular intersecondaries; irregular tertiary mesh; margin mostly entire, tips of lobes occasionally with minor lobes; texture coriaceous.

Discussion. Numerous specimens in the flora clearly indicate a relationship to the modern *Quercus lobata* Née, and closely resemble the smaller leaves produced by that species in the more semiarid parts of its range. The valley oak ranges southward from central California, where it forms a characteristic savanna association at lower elevations, into the northern parts of the southern California province.

Quercus duriuscula Knowlton as figured by Dorf from the Lower Idaho flora (1936) has been considered more nearly related to *Q. garryana* than to *Q. lobata.* Although Brown has placed this Idaho record in synonymy with *Q. pseudo-lyrata* Lesquereux (Brown, 1937*a*), it does not properly belong there, owing to its entire and rounded lobes.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1626; paratypes, nos. 1624, 1625; nos. 1627, 1628.

Quercus orindensis Dorf

(Plate 27, figure 5; plate 28, figures 2–5)

Quercus orindensis Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 89–90, pl. 9, figs. 6, 8, 9 (not fig. 7, which is *Q. douglasoides* Axelrod), 1930.

Quercus orindensis displays a general relationship to the Confusae and Lanceolatae groups of the southern Rocky Mountains and Mexico (Trelease, 1924), but its closest affinity seems to be with *Q. vaseyana* Buckley of western Texas and adjacent Mexico; *Q. vaseyana* is sometimes considered a variety of the more widely distributed *Q. undulata* Torrey. The writer has collected specimens of *Q. vaseyana* in the Edwards Plateau of west-central Texas which duplicate all characters shown by *Q. orindensis.* In this region it is a characteristic member of the oak-juniper community (Clements, 1920), which has a large representation in the later Tertiary of the western United States. The associates of *Q. vaseyana* include species of *Arbutus, Celtis, Cercis, Forestiera, Juniperus, Mahonia, Populus, Rhus,* and *Ungnadia,* all of which are represented by closely related plants in the Miocene and Pliocene floras of California and Nevada.

One of the specimens of *Quercus orindensis* figured by Dorf from the Sonoma formation (1930, pl. 9, fig. 7) is unquestionably related to the modern *Q. douglasii* Hooker and Arnott of California. This Sonoma specimen differs from the remainder, which come from the Mulholland locality, in two important respects: (*a*) the leaves of *Q. orindensis* are long and slender, whereas that of the Sonoma material is small and oval; (*b*) the leaf lobes in *Q. orindensis* are acute and directed forward, whereas in the Sonoma specimen they are blunt and often form right angles with the lobes above and below. This Sonoma material which is related to the modern *Q. douglasii,* together with the specimens of *Q. orindensis* from the Mount Eden flora, is accordingly assigned to a new species, *Q. douglasoides* Axelrod. This species, which has not yet been encountered in the Mulholland flora, is described in chapter 7 of this volume.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 360, 361, 362; plesiotypes, nos. 1617, 1618, 1619, 1620, 1621; nos. 1622, 1623.

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Quercus simulata Knowlton

Quercus simulata Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 728, pl. 101, figs. 3, 4; pl. 102, figs. 1, 2, 1898.

Condit, Carnegie Inst. Wash. Pub. 553, p. 45, pl. 5, fig. 3, 1944 (see synonymy).

Both entire-margined and serrate leaves in the flora correspond to the range in leaf variation of the modern *Quercus myrsinaefolia* Blume of eastern Asia. The Mulholland record is the first in the Pliocene of California for this characteristic Miocene species of the Columbia Plateau and northern Great Basin. All specimens are only slightly smaller than those figured by Dorf from the Lower Idaho flora (1936). Further collections may show that the Mulholland material should be recognized as a distinct later Tertiary species, being of the same category as *Populus lindgreni* and *P. pliotremuloides* (Chaney, 1938*a*, pp. 212–213).

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1629, 1630, 1631, 1632.

Quercus wislizenoides new species

(Plate 29, figures 4–9)

Quercus hannibali Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 86–88, pl. 8, figs. 8, 10 only, 1930.

Description. Leaves oval to rounded and elliptical; size varying from 4.4 cm. long and 3.2 cm. wide in the larger specimens, to 1.7 cm. long and 1.8 cm. wide in the smaller; apex rounded to apiculate; base rounded to obtuse; secondaries varying in numbers depending on leaf size, from 10 in the larger leaves to 4 in the smaller, departing at moderate but abruptly changing angles; intersecondaries weakly developed; coarse tertiary mesh, irregular; margin entire, occasionally with one or few teeth, or typically serrate; texture heavy and coriaceous, often crisped and curled.

Discussion. This is the dominant species of the Mulholland flora, and on the basis of more than 600 specimens, it seems undoubtedly referable to the living *Quercus wislizenii* A. DeCandolle. The interior live oak is common in the Upper Sonoran and Arid Transition zones of California, ranging from the northern end of the Great Valley southward into northern Baja California. Among its diverse habitats are border-redwood, digger pine, and desert border.

Examination of the two specimens of *Quercus hannibali* Dorf (1930, pl. 8, figs. 8, 10) from the Mulholland locality shows clearly that they are related to the modern *Q. wislizenii,* rather than to *Q. chrysolepis.* Only the specimen recorded from the Sonoma formation (*ibid.,* pl. 8, fig. 9) is retained as *Q. hannibali.*

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 354, 355, 356; plesiotypes, nos. 1633, 1634, 1635, 1636, 1637, 1638, 1639.

Family ULMACEAE

Celtis kansana Chaney and Elias

(Plate 30, figure 1)

Celtis kansana Chaney and Elias, Carnegie Inst. Wash. Pub. 476, I, pp. 38–39, pl. 5, figs. 1–5, 1936.

Condit, Carnegie Inst. Wash. Pub. 553, p. 77, pl. 14, fig. 4, 1944 (see synonymy).

The hackberry was reported first from this locality by Chaney and Elias (1936, p. 21). The nearest occurrence of its modern equivalent, *Celtis reticulata* Torrey, to

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the Mulholland area is in the southern Great Valley of California near Caliente. This is interpreted as a remnant of the Southwest American Element, which had a greater representation in central California in the Pliocene. Other relicts of similar origin now living in the same general region include *Isomeris arborea* Nuttall, *Larrea mexicana* Moricand, *Lepidospartum squamatum* Gray, and *Prosopis juliflora* DeCandolle.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1640.

Family BERBERIDACEAE

Mahonia marginata (Lesquereux) Arnold

Mahonia marginata (Lesquereux) Arnold, Contr. Mus. Paleontol. Univ. Mich., vol. 5, no. 4, pp. 64–65, 1936.

Odostemon marginata (Lesquereux) Knowlton, U. S. Geol. Surv. Prof. Paper 131*g*, p. 189, pl. 43, figs. 7–10, 1923.

Two small leaf impressions, one narrowly lanceolate and the other rounded and with sharp, long, and reflexed teeth, closely resemble those produced by the modern desert barberry, *Mahonia fremontii* (Torrey) Fedde, of southeastern California and regions to the south. In these areas it is found regularly in desert-border habitats and ranges upward into the pinyon-juniper association.

Exactly similar specimens have been collected recently at Mint Canyon and in the andesitic sediments near Oakdale (Mehrten formation). Further collections may show that *M. mohavensis* Axelrod of the Tehachapi flora only represents variation of this semiarid barberry.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1643, 1644.

Family LAURACEAE

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939 (see synonymy).

The California laurel, *Umbellularia californica* Nuttall, is a common tree along the stream at the fossil locality. The limited occurrence of its Pliocene equivalent, *U. salicifolia*, in the flora suggests that it has increased in abundance in the area since Mulholland time. The date of this invasion was perhaps during the late Pliocene and early Pleistocene. Other species in the flora which have been similarly interpreted include the madrone (*Arbutus*) and alder (*Alnus*).

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1645, 1646, 1647.

Family PAPAVERACEAE

Dendromecon reticulata new species

(Plate 30, figure 2)

Description. Leaf elliptic-lanceolate in outline, with an obtuse base, apex missing but apparently acute; 4.3 cm. long and 3.0 cm. wide (estimated); petiole heavy and firm, 2 mm. preserved; wavering secondaries departing at 35° to 45°, looping upward along the margin, joining to the secondaries above by a complex system of bifurcating tertiaries; a thin marginal vein passing upward for over 1 cm., joining the margin by tertiaries and the secondary above by a complex system of tertiaries;

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tertiaries conspicuous and irregular; nervilles not preserved; margin entire; texture thick and coriaceous.

Discussion. This is the first record of the genus *Dendromecon* in fossil deposits. Its rarity as a fossil may be attributed largely to its preference for dry upland sites, removed from areas of accumulating sediments. The fossil species is clearly related to the common bush poppy, *Dendromecon rigida* Bentham, which is characteristic on dry hill slopes and rocky soils from the inner north Coast Ranges and lower Sierra Nevada southward into Baja California.

It is significant that this species has been encountered in the modern flora at one or two isolated localities in southern Arizona. Other typical Californian species with relict occurrences in southern Arizona include *Fremontia californica* Torrey and *Rhus integrifolia* Bentham and Hooker. The writer has already pointed out the similarity between the vegetation of southern California and that of southern Arizona, and has presented evidence for the general conclusion that the floras of these two areas are related in origin (Axelrod, 1939). The occurrence of *Dendromecon* in southern Arizona emphasizes further the affinities between these floras, and suggests a north Mexican origin for the genus.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1642.

Family PLATANACEAE

Platanus paucidentata Dorf

Platanus paucidentata Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 94–96, pl. 10, figs. 4, 9; pl. 11, fig. 1; pl. 12, fig. 1, 1930.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 48–49, pl. 9; pl. 10, fig. 4; pl. 11, fig. 5, 1944 (see synonymy).

Leaves of this common Pliocene sycamore are numerous in the flora and are clearly related to the modern *Platanus racemosa* Nuttall of central and southern California. Sycamore no longer exists at the fossil locality, but has been restricted to hotter and drier inland areas not far to the east. The affinities and past distribution of *P. paucidentata* have been discussed elsewhere (Axelrod, 1939, p. 105).

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1648.

Family ROSACEAE

Amelanchier sp. Dorf

Amelanchier sp. Dorf, Carnegie Inst. Wash. Pub. 412, I, p. 100, 1930.

A single poorly preserved small leaf impression appears to represent *Amelanchier*, and is referred tentatively to the Pliocene species reported by Dorf and by Hannibal from the Santa Clara flora. These leaves from the Pliocene of California are much smaller than those of the Miocene species recorded from the northern Great Basin.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1649.

Cercocarpus cuneatus Dorf

Cercocarpus cuneatus Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 98–99, pl. 12, fig. 3, 1930.
Axelrod, Carnegie Inst. Wash. Pub. 553, p. 101, 1944 (see synonymy).

A leaf impression of *Cercocarpus* differs in no essential respect from the Mount Eden and Santa Clara material. Because *C. cuneatus* is now represented by only

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3 specimens, it is not possible to determine its exact relationship to *C. antiquus* Lesquereux; all specimens of *C. cuneatus* resemble only the smaller leaves of *C. antiquus*. Until more material becomes available so that the range of variation of *C. cuneatus* is more clearly understood, it is retained as distinct from *C. antiquus*. Both species closely resemble leaves produced by the modern *C. betuloides* Nuttall of the western United States.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1650.

Chamaebatia prefoliolosa Brown

Chamaebatia prefoliolosa Brown, Jour. Paleontol., vol. 9, p. 578, pl. 69, fig. 4, 1935.

A part of a tripinnatifid leaf shows that this species is closely related to the modern *Chamaebatia foliolosa* Bentham of the Sierran Transition forest. Associated with the Miocene forest flora of the Columbia Plateau, which contains elements of both the coast redwood and the Sierran Transition forests, this species appears to have been segregated from the redwood forest since later Pliocene time, as suggested by Mason (1936, p. 188).

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1651.

Lyonothamnus mohavensis Axelrod

(Plate 30, figures 3–5)

Lyonothamnus mohavensis Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 107–108, pl. 8, figs. 6, 9, 1939.

Leaves of the Pliocene species are of intermediate size between the modern *Lyonothamnus floribundus* Gray and the Miocene *L. mohavensis*. This fact is consistent with the suggestion that the species has become adapted gradually to coastal conditions since the Middle Tertiary. In this connection it may be recalled that another insular species, *Quercus tomentella,* related to the fossil *Q. declinata,* also shows an increase in leaf size from the Miocene to the present. It seems desirable to obtain additional material before describing these Pliocene species as distinct.

Lyonothamnus is now known to have had a wide distribution in California and Nevada during middle and later Tertiary time (Axelrod, 1940*d*). When this fact is considered together with the existence of additional insular endemics whose fossil distribution is of a similar type, there seems to be evidence for believing that other endemic insular species, as yet unrecorded in the fossil record, may also have had a similar history.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1652, 1653, 1654.

Photinia sonomensis new species

Heteromeles sp. Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 99–100, pl. 12, fig. 2, 1930.
Photinia (*Heteromeles*) sp. Dorf. Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 108–109, pl. 8, fig. 10, 1939.
Quercus hannibali Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 86–88, pl. 8, fig. 11 only, 1930.

Reported originally from the Sonoma formation, *Photinia* (*Heteromeles*) has been encountered at two additional localities in the past few years. It now seems desirable to assign a specific name to *Photinia* (*Heteromeles*) sp. Dorf, since adequate material is available for study.

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Description. Leaves typically oblong, rounded to acute above and below, up to 5.0 or 6.0 cm. long and 2.0 to 2.5 cm. wide; heavy midrib and thick petiole; alternate secondaries diverging at moderate to high angles, looping within the margin, camptodrome, commonly wavering; intersecondaries typically present; tertiaries coarse and irregular; teeth small and sharp, moderately to rather widely spaced; texture coriaceous.

Discussion. This species is considered to represent the fossil equivalent of *Photinia arbutifolia* Lindley (*Heteromeles arbutifolia* Roem.), a common California shrub. Although the latter attains best development in the semiarid parts of California, where it is a chaparral component, it occurs also on the borders of the redwood forest in central California.

The fossil species is now known from the Sonoma, Mulholland, Oakdale, and Tehachapi floras. *Photinia* is represented also in the Alvord Creek flora of southern Oregon, but that species may be distinct. The oak listed in the synonymy above was incorrectly figured. It is the upper half of a coriaceous leaf; the character of its looping secondaries, intersecondaries, and teeth indicates that it is properly referable to *Photinia.* It should be noted that this particular specimen comes from the Mulholland locality where *Photinia* is common.

The specimen figured by Dorf from the Sonoma flora is designated the type of *Photinia sonomensis.*

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 390; nos. 1655, 1656.

Prunus moragensis new species

(Plate 30, figures 6, 8, 10)

Description. Leaves lanceolate to broadly ovate; 2.9 to 3.1 cm. long and 1.8 to 2.0 cm. wide; petiole up to 1.0 cm. long; relatively thin alternate secondaries, diverging at moderate to low angles, subcamptodrome; tertiaries irregular; margin serrulate, texture thin. Seed ovoid; 9 mm. long and 6 mm. wide; with a ridge along one side.

Discussion. This material clearly represents *Prunus,* and among living species it is closely related to *P. emarginata* (Douglas) Walpers, a widely distributed shrub in western North America. The bitter cherry is a common associate of the coniferous forests in the western United States, but ranges also into the more xeric communities at the south. In central and southern California it may occur along streams in the chaparral-oak country.

The only other material seen by the writer that is referable to *Prunus moragensis* and the modern *P. emarginata* consists of specimens from the Truckee formation in western Nevada.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1657, 1658, 1659.

Prunus prefasciculata Axelrod

Prunus prefasciculata Axelrod, Carnegie Inst. Wash. Pub. 516, p. 110, pl. 8, figs. 13, 14, 1939.

Obovate leaf impressions, with long, thin secondaries becoming camptodrome in the upper part of the blade, show relationship to the modern *Prunus fasciculata* Gray. This species is common in desert and desert-border washes in southeastern California, ranging eastward through southern Nevada into Utah and Arizona. It occurs in interior southern California and ranges northward as isolated colonies into the Kern River canyon and south Coast Ranges east of San Luis Obispo. Like other typically southern plants, such as *Celtis reticulata, Forestiera neo-mexicana, Quercus*

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palmeri, and *Rhus laurina,* which range north of southern California or desert regions, this species is interpreted as a relict of the Pliocene invasion of central California by the Madro-Tertiary Flora.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1660, 1661.

Family ANACARDIACEAE

Rhus franciscana new species

(Plate 30, figures 9, 11)

Description. Leaflets long oval, lobed and asymmetrical, rounded above and acute below; 1.9 to 3.4 cm. long and 1.1 to 1.9 cm. wide, greatest width in the lower part; petiolules appear sessile; midrib firm and curved; alternate secondaries diverging at 30° to 55°; tertiaries not preserved; lobed margin, occasionally with blunt teeth; texture firm.

Discussion. These small leaflets are clearly of the type produced by the modern *Rhus diversiloba* Torrey and Gray in areas of its drier distribution, a fact consistent with the semiarid nature of the associated flora. It is to be expected that a species of poison oak from the Miocene floras at the north will be found to differ from *R. franciscana* in having a thinner texture and larger size. On this basis, the species will have stratigraphic value comparable with that of such forms as *Populus lindgreni* and *P. pliotremuloides,* or *Populus eotremuloides* and *P. alexanderi* (Chaney, 1938*a,* pp. 212–213).

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1664, 1665.

Rhus moragensis new species

(Plate 31, figures 7, 9)

Description. Leaves ovate, apex acute to blunt, base broadly cuneate to subcordate; 2.9 cm. long and 2.4 to 3.0 cm. wide; petiole stout, 1.1. cm. long; midrib firm and straight; numerous alternate secondaries departing at 45° to 60°, wavering slightly in their outward course, bifurcating once or twice near the margin, passing into the margin or looping upward within it; tertiaries irregular and poorly preserved, apparently disappearing in the intersecondary areas; finer nervilles not preserved; margin entire; texture thick and coriaceous.

Discussion. These impressions clearly resemble those of the modern *Rhus ovata* Watson, a characteristic chaparral member in southern California. The eastward extension of this species into southern Arizona clearly suggests its Sierra Madrean origin, an inference consistent also with the nature of its associate species both past and present. Many of its associates in southern California and southern Arizona have fossil equivalents in the Mulholland flora. It may be pointed out that the resemblance of the fossil to *R. ovata* is shown not only in the shape and venation, but in the characteristic folding of the leaf.

Rhus preovata Chaney from the Crooked River flora (Chaney, 1927) differs from this species in its thinner texture, pli-nerved venation, and adaxial secondaries departing from the primaries, and in the character of the finer nervation. *Rhus preovata* seems to be leguminous, not anacardiaceous, and may be matched in a general way by such genera as *Dolichos, Phaseolus,* and *Rynchosia.*

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1666, 1667.

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Rhus prelaurina Axelrod

Rhus prelaurina Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 180–181, pl. 6, fig. 12, 1937.

First recorded as *Rhus* sp. by Dorf (1930, pp. 100–101, pl. 12, fig. 4) from the Mulholland flora, this species has since been found in the Mount Eden and Mint Canyon floras of southern California. The fossil species resembles the modern *Rhus laurina* Nuttall, a common coastal chaparral-sagebrush shrub ranging from Santa Barbara southward into northern Baja California. An outpost occurrence of the species in the Coast Ranges 100 miles north of Santa Barbara is a critical one. It is regarded as a relict of the southern continental flora which had a wider representation in central California in the early Pliocene.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 394, 1668.

Family ACERACEAE

Acer bolanderi Lesquereux

Acer bolanderi Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 27, pl. 7, figs. 7–11, 1878.

Several specimens in the Mulholland flora are similar to the maple from the Table Mountain flora. Greatest affinity is apparent with *Acer grandidentatum* Nuttall of the southern Rocky Mountain region, an area where many of the modern equivalent Mulholland species are to be found. In his *Silva of North America,* Sargent has considered *A. grandidentatum*, as well as *A. leucoderme* Small and *A. floridanum* Pax, which show a general relationship to *A. bolanderi,* to be varieties of *A. saccharum* Marsh. If these species are closely related, as they appear to be, it may be suggested that this phylad developed from the early Tertiary equivalent of *A. saccharum,* which spread southward from a holarctic center of distribution.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1662, 1663.

Family SAPINDACEAE

Sapindus oklahomensis Berry

(Plate 31, figures 1, 2)

Sapindus oklahomensis Berry, Proc. U. S. Nat. Mus., vol. 54, pp. 632–633, pl. 95, figs. 1, 2, 1918.

Chaney and Elias, Carnegie Inst. Wash. Pub. 476, I, p. 43, pl. 7, figs. 1–3, 1936.

Brown, Jour. Wash. Acad. Sci., vol. 30, p. 355, 1940 (see synonymy).

Sapindus lamottei Axelrod, Carnegie Inst. Wash. Pub. 476, III, p. 181, pl. 6, fig. 6, 1937.

Salix sp. Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 79–80, pl. 8, fig. 3, 1930.

Numerous asymmetrical leaflets in the flora are unquestionably referable to this species, which is related closely to the modern *Sapindus drummondii* Hooker and Arnott of the southwestern United States and adjacent areas. The discovery of a leaf fragment in the Mount Eden collections makes it desirable to place *S. lamottei,* which was founded on seed material, in synonymy with *S. oklahomensis.* The willow listed above is from the Mulholland locality, and represents a slender leaflet of *Sapindus.*

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 339, 1669, 1670, 1670*a* (counterpart); no. 1671.

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Family RHAMNACEAE

Berchemia multinervis (Al. Braun) Heer

Berchemia multinervis (Al. Braun) Heer, Flora tertiaria Helvetiae, vol. 3, p. 77, pl. 123, figs. 9–18, 1859.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 52–53, pl. 12, fig. 4, 1944 (see synonymy).

Several specimens in the Mulholland flora are referred tentatively to this species, which has been recorded in the transitional Mio-Pliocene Neroly, Remington Hill, and Table Mountain floras of mid-central California. These leaves resemble those produced by the modern *Berchemia scandens* Trelease of the eastern United States, but they are similar also to *Karwinskia humboldtiana* Zuccarini of the southwestern United States and Mexico. Condit has discussed the taxonomic relationships of these rhamnaceous genera (chap. 2 above, pp. 52–53), and is of the opinion that they are not greatly different. He suggests that *Karwinskia* represents a segregate of *Berchemia* which developed at the south in response to aridity in Middle Tertiary time.

Still another explanation is suggested by the present distribution of the genus *Karwinskia,* which, in addition to the southwestern United States and Mexico, includes such tropical and subtropical regions as Central America, South America, and the West Indies. Such a distribution suggests that *Karwinskia* might originally have been a member of the subtropical vegetation that spread northward in Eocene time. On this basis, *Berchemia* could have differentiated at the north from an originally low-latitude genus, and thence spread southward with the Tertiary redwood forest. In connection with this suggestion of the derivation of *Berchemia* from *Karwinskia,* it is significant that the flowers of *Berchemia* have definitely derivative features as compared with *Karwinskia.*

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1672, 1673, 1689.

Ceanothus prespinosus new species

(Plate 31, figure 3)

Description. Leaves oval, rounded above and below, occasionally acute; 1.7 to 3.0 cm. long and 1.1 to 1.7 cm. wide; only the base of a thick petiole preserved; midrib firm, heavy below, thinner above, and displaced by the secondaries in the upper part of the blade; alternate secondaries departing at 40° to 55° and looping upward, becoming camptodrome; tertiaries largely at right angles to secondaries; margin entire; texture firm.

Discussion. This species is closely related to the modern *Ceanothus spinosus* Nuttall, which is a characteristic constituent of the dense chaparral of the coastal region, from the southern Santa Lucia Mountains southward into San Diego County.

It is distinct from the several recently described species in the later Tertiary of western North America.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1674; nos. 1675, 1676.

Rhamnus moragensis new species

(Plate 30, figure 7)

Description. Leaf broadly rounded elliptic, tip subtruncate and base nearly subcordate; 1.3 cm. long and 1.6 cm. wide (estimated); petiole missing but apparently

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short and heavy; midrib heavy; alternate thin secondaries departing at 65° to 80°, apparently looping upward but becoming obscured in the outer part; margin sharply serrulate; texture heavy.

Discussion. This fossil species is closely related to the modern *Rhamnus crocea* Nuttall, a common California shrub. At the north it occurs along the borders of the redwood forest and in oak or chaparral communities, and southward it is common in the chaparral. A related species occurs also in southern Arizona, where it has many chaparral and woodland associates which have equivalent fossil species in the Mulholland flora.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1677.

Rhamnus precalifornica Axelrod

Rhamnus precalifornica Axelrod, Carnegie Inst. Wash. Pub. 516, p. 122, pl. 11, figs. 1, 2, 1939.

Several impressions can be referred without hesitation to this species, which is related to the modern *Rhamnus californica* Eschscholtz. This is a widely distributed species, ranging from California eastward into Texas and southward into Mexico. Many varieties have been recognized, whose diverse habitats include the redwood forest and the borders of the desert.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1678, 1679.

Family STERCULIACEAE

Fremontia lobata Axelrod

(Plate 31, figure 4)

Fremontia lobata Axelrod, Carnegie Inst. Wash. Pub. 516, p. 123, pl. 11, figs. 8, 10, 1939.

Several specimens differ in no essential respect from the leaves produced by the modern *Fremontia californica* Torrey. This large shrub ranges from central California southward into Baja California, and occurs also in southern Arizona. Attaining optimum development in the chaparral of southern California and in the southern Sierra Nevada, *Fremontia* also borders the redwood forest in areas of its more northerly distribution.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1680; no. 1681.

Family CORNACEAE

Cornus ovalis Lesquereux

Cornus ovalis Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 23, pl. 6, figs. 1, 2, 1878.

Two leaf impressions with secondaries looping well into the apex are clearly referable to dogwood and are assigned to the Table Mountain species, which they closely resemble. Although it is difficult to determine the relationship of this material to modern species, affinity to such species as *Cornus californica* C. A. Mey and *C. glabrata* Bentham is apparent.

It is probable that the specimen figured from the Latah flora (Brown, 1937*a*) is a different species, for it is said to resemble *Cornus nuttallii* Audubon, which has much larger leaves than *C. ovalis.*

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1682, 1683.

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Nyssa elaenoides (Lesquereux) Condit

(Plate 31, figure 5)

Nyssa elaenoides (Lesquereux) Condit, Carnegie Inst. Wash. Pub. 553, pp. 86–87, pl. 18, figs. 1, 4; pl. 20, fig. 7, 1944 (see synonymy).

A single well preserved leaf in our collection is closely similar to those of the modern *Nyssa sylvatica* Marshall of eastern North America. Distributed from Ontario and Maine southward into Florida and westward into Texas and Oklahoma, this modern species not only occurs along the borders of swamps, but ranges also into hilly regions. In areas of its western distribution, as in Oklahoma, it occurs in pine-oak forests, a habitat more nearly consistent with the Mulholland occurrence than the deep, rich, swampy soils required by *N. aquatica* and its fossil equivalent, *N. knowltoni*.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1684.

Family ERICACEAE

Arbutus matthesii Chaney

Arbutus matthesii Chaney (in part), Carnegie Inst. Wash. Pub. 346, IV, pp. 131–132, pl. 20, figs. 1, 5 (not figs. 3, 4, which are *Nyssa elaenoides* (Lesquereux) Condit), 1927.

Arbutus matthesii is regularly represented in the later Miocene floras of the northern Great Basin and Columbia Plateau, and is closely related to the modern *A. menziesii* Pursh of the Pacific coast. Although madrone is common at the fossil locality today, the occurrence of only one leaf impression of its Pliocene representative in the Mulholland flora suggests that it lived remote from the immediate basin of deposition.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1686.

Arctostaphylos moragensis new species

(Plate 31, figure 8)

Description. Leaf oval, rounded above and apparently acute below; about 3.0 cm. long and 2.1 cm. wide; midrib firm and curved; petiole missing; alternate secondaries, thin, departing at low angles, wavering in the outer parts; tertiaries not preserved; margin entire; texture heavy and coriaceous.

Discussion. A poorly preserved specimen is clearly referable to manzanita. Although certain modern species cannot be distinguished easily by their leaves, it is to be pointed out that the modern *Arctostaphylos glandulosa* Eastwood produces leaves closely similar to the fossil. From a paleoecological standpoint it is significant that this species is a regular associate of all the modern equivalents of the Mulholland species now in California, for it ranges from the redwood forest southward into San Diego County.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1687.

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Family OLEACEAE

Fraxinus caudata Dorf

Fraxinus caudata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 106–107, pl. 13, fig. 8 (not figs. 6, 7, which are *Persea coalingensis* (Dorf) Axelrod), 1930.

Only one occurrence of the modern equivalent of this species, *Fraxinus oregona* Nuttall, is known from the east side of San Francisco Bay, and this is near Walnut Creek, several miles east of the fossil locality.

It has been pointed out elsewhere in this paper that two of the cotypes of *Fraxinus caudata* (Dorf, 1930, pl. 13, figs. 6, 7) represent *Persea* rather than ash.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1688.

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PLATES 24—31

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FIG. 1. General view of Mulholland locality, P386, in railroad cut in lower center of picture.

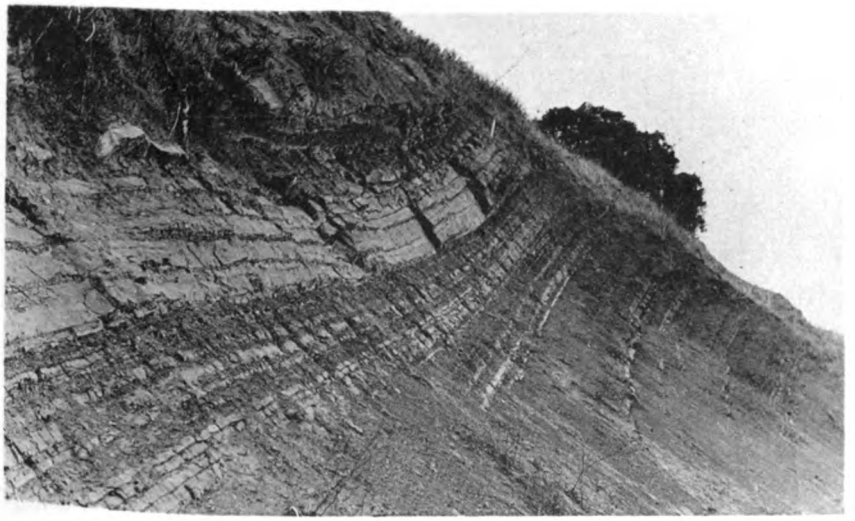

FIG. 2. The plant-bearing strata at locality P386

MULHOLLAND LOCALITY

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FIG. 1. Stream-bank vegetation in the inner Santa Cruz Mountains

FIG. 2. Slope vegetation in the inner Santa Cruz Mountains

LIVING EQUIVALENT MULHOLLAND VEGETATION

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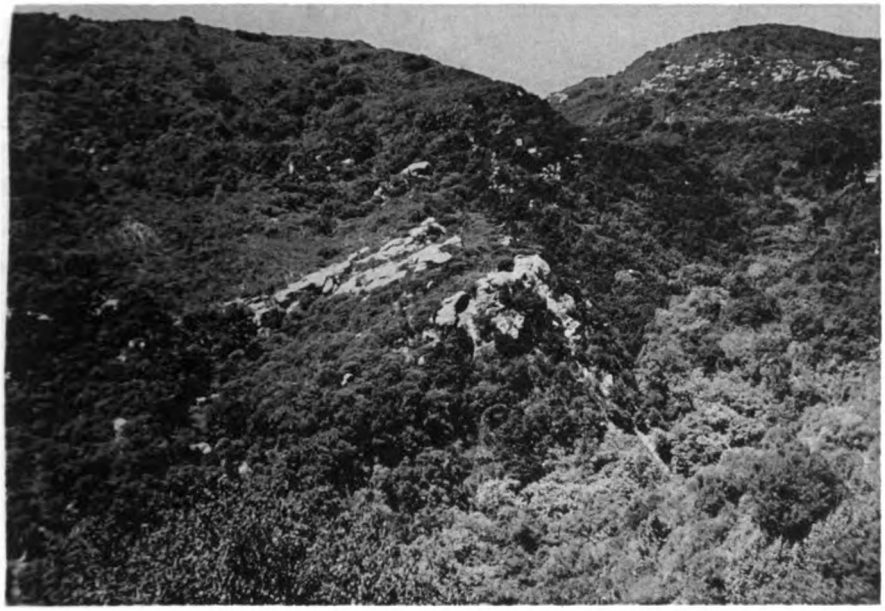

FIG. 1. Chaparral in the Santa Ynez Mountains

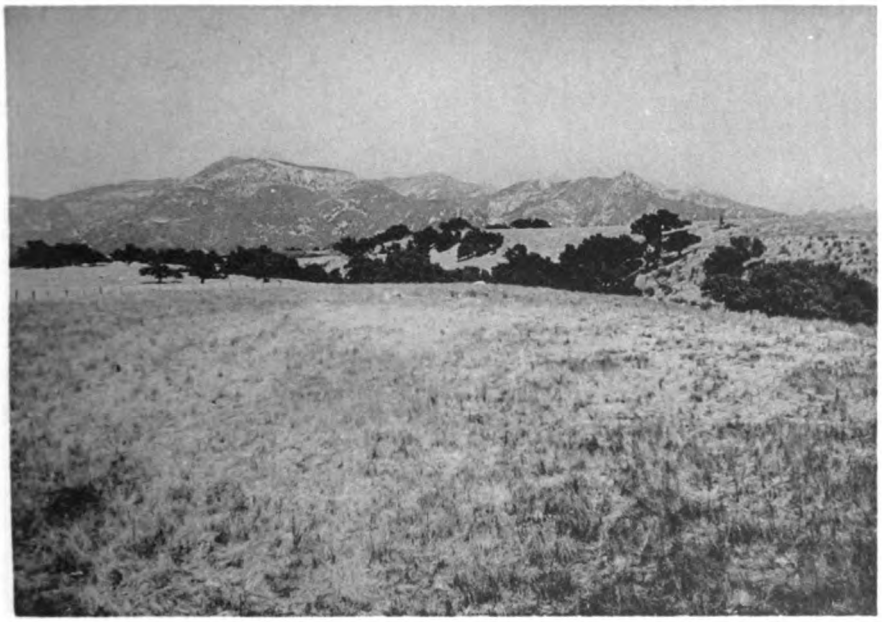

FIG. 2. The Santa Ynez Mountains near Santa Barbara, California

LIVING EQUIVALENT MULHOLLAND VEGETATION

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PLATE 27

MULHOLLAND FOSSILS

PAGE

FIGS. 1, 3. *Populus parce-dentata* (Lesquereux) Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1598, 1599 129

FIGS. 2, 4. *Populus prefremontii* Dorf. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1602, 1603 130

FIG. 5. *Quercus orindensis* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1621 135

FIG. 6. *Alnus merriami* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1610 133

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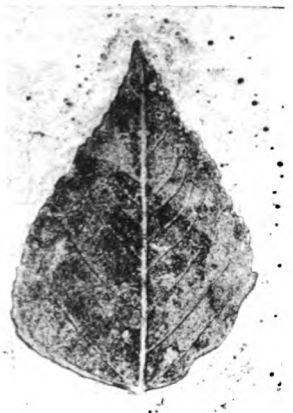

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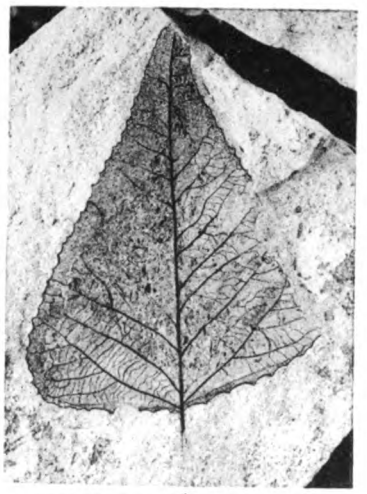

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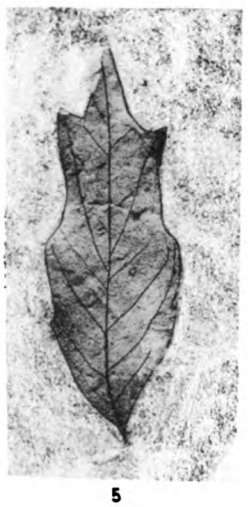

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PLATE 28

MULHOLLAND FOSSILS

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FIG. 1. *Populus prefremontii* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1601 130

FIGS. 2–5. *Quercus orindensis* Dorf. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1618, 1617, 1619, 1620 135

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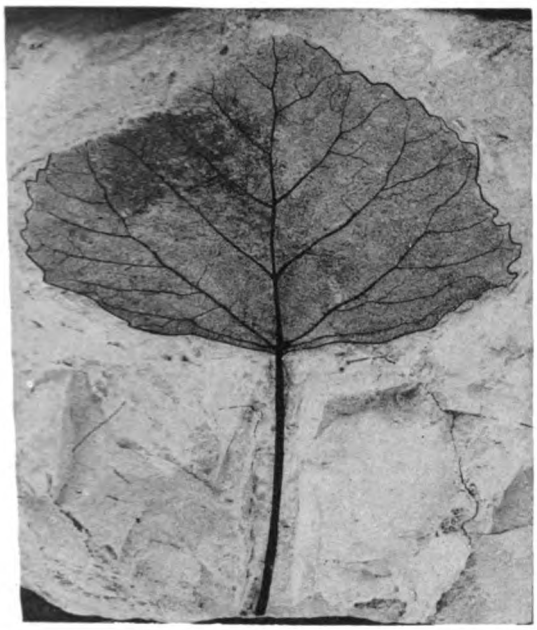

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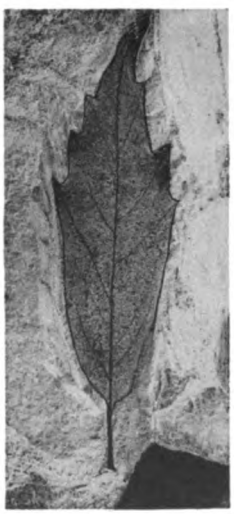

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PLATE 29

MULHOLLAND FOSSILS

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FIG. 1. *Quercus moragensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1626 134

FIGS. 2, 3. *Quercus moragensis* Axelrod. Paratypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1624, 1625 134

FIGS. 4–9. *Quercus wislizenoides* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1634, 1635, 1637, 1633, 1638, 1636 136

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PLATE 30

MULHOLLAND FOSSILS

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FIG. 1. *Celtis kansana* Chaney and Elias. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1640 136

FIG. 2. *Dendromecon reticulata* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1642 137

FIGS. 3, 4. *Lyonothamnus mohavensis* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1654, 1653 139

FIG. 5. *Lyonothamnus mohavensis* Axelrod. Plesiotype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 1652 139

FIGS. 6, 8, 10. *Prunus moragensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1657, 1658, 1659 140

FIG. 7. *Rhamnus moragensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1677 143

FIG. 9. *Rhus franciscana* Axelrod. Cotype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 1664 141

FIG. 11. *Rhus franciscana* Axelrod. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 1665 141

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PLATE 31

MULHOLLAND FOSSILS

PAGE

FIGS. 1, 2. *Sapindus oklahomensis* Berry. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., nos. 1670, 1669 142

FIG. 3. *Ceanothus prespinosus* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1674 143

FIG. 4. *Fremontia lobata* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1680 144

FIG. 5. *Nyssa elaenoides* (Lesquereux) Condit. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1684 145

FIG. 6. *Castanopsis perplexa* (Knowlton) Brown. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1611 133

FIGS. 7, 9. *Rhus moragensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1666, 1667 141

FIG. 8. *Arctostaphylos moragensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1687 145

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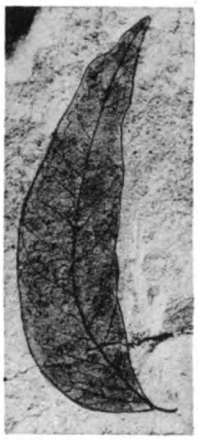

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6

The Oakdale Flora

DANIEL I. AXELROD

Introduction

The discovery of a flora of determinable age in the lower foothills of the central Sierra Nevada east of Oakdale is particularly significant in relation to investigations now under way on the Pliocene of the western United States. The study of several floras from the Coast Ranges to the west is completed in the present volume, and a preliminary statement has been made on several others east of the Sierra (Axelrod, 1940*b*). Intermediate in geographic position between these, the Oakdale flora throws light on the distribution and local differentiation of later Tertiary floras in western North America.

The writer's present studies are an attempt to build up a complete sequence of floras of Pliocene age in the several paleobotanical provinces of the western United States. These provinces represent regions of comparatively uniform climatic and topographic character, having similar climax vegetation, but their general outlines are only partly understood. Three have already been recognized in the Lower Pliocene of the Great Basin (Axelrod, 1940*b*), and such areas as the San Francisco Bay region, the lower central Sierran slopes, and southern California apparently represent others. By determining the sequence of floras in each of these provinces during the later Tertiary, it is possible not only to establish a basis for correlation of the deposits in which they occur, but to determine also the sources of origin of their several elements, and their paths of migration both before and since the Pliocene. Such an approach to the study of Pliocene floras is the more appropriate because these later Tertiary assemblages are highly localized in development, with a great diversity in composition among provinces. On the other hand, the forests of the early and middle Tertiary may be correlated rather readily over wider areas on the basis of their similar floristic and specific content, because the forest provinces of these epochs were relatively large. It was not until later Miocene time in the western United States that the forest zones were disrupted by mountain building and climatic change to form the narrow and restricted provinces of the later Tertiary, and during the Pliocene these areas were delimited further. Thus the facies problem presented by Pliocene vegetation in the western United States may be solved only by determining the complete floristic sequence in the several provinces of the region. Through recognition of the gradual modification of the Arcto-Tertiary Flora in response to increasing aridity (Chaney, 1936*a*, 1938*a*, 1938*b*), and by determining the time of appearance of the semiarid Madro-Tertiary Flora as an important floristic group in the various provinces (Axelrod, 1938, 1939, 1940*a*,

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1940*b*), it is believed that interprovincial correlation may be accomplished more readily.

The Oakdale flora was collected first by a class in field geology from the University of California under the direction of Howel Williams, during the spring of 1936. For assistance in securing additional material, the writer is indebted to James F. Ashley. Data with respect to the stratigraphic relations of the flora to the Oakdale fauna in the near-by region have been generously supplied by Hugo F. Goeriz, who has collected the fauna and studied it with R. A. Stirton (1942).

Geologic Occurrence

In late Upper Miocene time extensive andesitic eruptions broke out along the summit region of the central Sierra Nevada. The andesitic detritus carried westward from this upland volcanic terrain as fluviatile sediments and mudflows to the lower flanks of the range has been mapped as the Mehrten formation in the Mokelumne District (Piper *et al.*, 1939). Piper and his associates have pointed out that these deposits, which have a low westerly dip of 2° to 3° and attain a thickness of 400 to 500 feet in the lower foothill region, extend north and south of the Mokelumne area for many miles. In reviewing the evidence regarding the age of the Mehrten formation, they concluded that the fine tuffaceous deposits containing *Pliohippus tantalus* in the region 4 miles east of Oakdale (VanderHoof, 1933) correspond to the uppermost part of the formation at its type section 30 miles north. The Oakdale flora occurs 3 miles southeast of this vertebrate locality, and in andesitic deposits lithologically identical with the Mehrten formation. The name Oakdale has been applied to the flora because it is stratigraphically near the Oakdale fauna, of which the *Pliohippus tantalus* locality is a part (Stirton and Goeriz, 1942).

The plant locality lies in the Stanislaus River valley at an elevation of 250 feet, 7 miles east of Oakdale and 3 miles southwest of Knights Ferry. (See pl. 32, fig. 1.) The coarse, andesitic, pumiceous tuff containing the flora crops out in a small quarry on the south slope of a swale near the middle of the southern border of Sec. 36, T. 1 S., R. 11 E., Copperopolis Quadrangle. The following section is exposed at locality P3628:

Soil	*Thickness* *Feet*	*Inches*
Conglomerate of rounded andesitic pebbles and bedrock material	1	6
Light-gray to blue-gray andesitic sandstone	6	10
Poorly bedded gray tuff containing pebbles of bedrock material and small pumiceous lapilli. Infrequent leaf impressions lying at various angles to a poorly defined bedding plane	2	9
Gray-brown cross-bedded coarse andesitic sandstone	7	0
Clean, light-gray fine-grained sandstone, locally coarser above	8	4
Light-gray to buff ashy clay, containing small sand and gravel lenses	1	2
Brownish-gray andesitic sandstone, with scattered pebbles	2	0
Base of exposure in creek bed		
Total	29	7

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The present position of the flora at an elevation of 250 feet is considered to represent approximately its original level of deposition. Late Cenozoic uplift, which amounted to over 5000 feet in the Sierra Nevada at the east, is not considered to have materially affected this region, which lies 2 miles west of the edge of the Sierra Nevada block bordering the Great Valley. The ultimate source for the greater part of the andesitic Mehrten deposits of the central Sierran foothill area, which includes siltstones, sandstones, conglomerates, breccias, mudflows, and tuffs, was in the volcanoes of the high Sierra Nevada.[1] The sediments which make up the formation are clearly of fluviatile origin, for they reveal the characteristic features of stream cross-bedding and channeling and contain heavy lenticular conglomerates. Although the breccias in the higher parts of the range seem to represent mudflows, in the lower foothill area they appear to have been transported from the higher mountains as the outwash of torrential floods. At many places they are interbedded with or underlain by lenses of well rounded cobbles and gravels (Piper *et al.*, 1939, p. 64).

The deposition of andesitic detritus over the lower Sierran slope gradually built up a pediment traversed by numerous distributary streams radiating from the major valleys. By the end of Mehrten time this aggradational plain, which had an average westerly slope of 90 to 100 feet per mile (*ibid.*, p. 70), covered the lower flanks of the range and spread westward into the Great Valley. The bulk of this material came from the high Sierra Nevada, but some of it may have been derived from vents in the foothill region. Vents of this type have been reported at Golden Gate Hill and Jackson Butte, near the towns of Jackson and Mokelumne Hill, 40 and 50 miles north of the Oakdale locality (Turner, 1894, p. 4; Piper *et al.*, 1939, p. 67). Detailed geologic mapping in the area east of Oakdale may disclose other sources for lowland andesitic eruptions. But judging from their rarity elsewhere on the lower Sierran slopes, cones in this area would presumably have been local in occurrence, and their contribution to the pediment which was being built up along the lower flanks of the range would have been of minor amount.

The fluviatile andesitic sediments containing the Oakdale flora are thus considered largely to represent material transported from areas of volcanism in the higher parts of the range, 40 and 60 miles eastward. The nature of preservation of the fossil leaves suggests that some of them may have been carried for long distances, for small, broken leaf fragments are commonly present in the plant horizon. The well preserved and complete leaves were presumably shed by plants located near the immediate site of deposition. Many of these are twisted and lie at various angles to the poorly defined bedding plane, as though they had been carried along by slowly moving sediments. Others are curled in such a manner as to suggest that they were dried by the sun and wind before they were blown into the accumulating sediments, and that deposition at times may have been subaerial.

[1] Cordell Durrell has recently discovered evidence suggesting that the Sierran mudflows may have been erupted from dikes in the summit region ("Andesite breccia dikes near Blairsden, Plumas County, California," paper presented before the Geological Society of America, Cordilleran Section, April 17–18, 1942).

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Composition and Physical Indications

The Oakdale flora as now known comprises 16 species of dicotyledons. All these except *Arctostaphylos oakdalensis* and *Ribes mehrtensis* have been reported previously from Pliocene floras in the western United States.

Systematic List of Species

Spermatophyta
- Angiospermae
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Populus alexanderi Dorf
        - Populus parce-dentata (Lesquereux) Axelrod
        - Populus pliotremuloides Axelrod
        - Salix wildcatensis Axelrod
    - Fagales
      - Fagaceae
        - Quercus dispersa (Lesquereux) Axelrod
        - Quercus cf. douglasoides Axelrod
        - Quercus wislizenoides Axelrod
    - Urticales
      - Ulmaceae
        - Celtis kansana Chaney and Elias
    - Ranales
      - Berberidaceae
        - Mahonia marginata (Lesquereux) Arnold
      - Lauraceae
        - Umbellularia salicifolia (Lesquereux) Axelrod
    - Rosales
      - Saxifragaceae
        - Ribes mehrtensis new species
      - Rosaceae
        - Photinia sonomensis Axelrod
      - Leguminosae
        - Robinia californica Axelrod
    - Sapindales
      - Sapindaceae
        - Sapindus oklahomensis Berry
    - Rhamnales
      - Rhamnaceae
        - Ceanothus precuneatus Axelrod
    - Ericales
      - Ericaceae
        - Arctostaphylos oakdalensis new species

Owing to the fact that leaf impressions are rare in the sediments, it has not been possible to determine the relative abundance of the various plants in the flora. Judging from about 200 specimens, the following 6 species appear to have

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been sufficiently common in the general vicinity of the fossil locality to contribute the preponderance of leaves to the deposit:

Mahonia marginata	Ribes mehrtensis
Populus alexanderi	Robinia californica
Quercus wislizenoides	Sapindus oklahomensis

Of these, *Quercus wislizenoides, Populus alexanderi,* and *Sapindus oklahomensis* are most abundant in the order listed.

Table 15, which lists the elements and components of the Oakdale flora, provides a basis for interpreting the physical conditions of Oakdale time. Since the flora is made up largely of members of the Oak woodland and Chaparral Components of the Southwest American Element, it is clear that a study of modern oak woodland and chaparral vegetation provides an index to Oakdale conditions.

TABLE 15

ELEMENTS AND COMPONENTS OF THE OAKDALE FLORA

Fossil species	*Equivalent living species*
Southwest American Element	
Oak woodland Component	
Celtis kansana	C. reticulata Torrey
Quercus cf. douglasoides	Q. douglasii Hooker and Arnott
Quercus wislizenoides	Q. wislizenii A. DeCandolle
Ribes mehrtensis	R. quercetorum Greene
Robinia californica	R. neo-mexicana Gray
Salix wildcatensis	S. lasiolepis Bentham
Sapindus oklahomensis	S. drummondii Hooker and Arnott
Chaparral Component	
Arctostaphylos oakdalensis	A. mariposa Dudley
Ceanothus precuneatus	C. cuneatus Nuttall
Mahonia marginata	M. fremontii (Torrey) Fedde
Photinia sonomensis	P. arbutifolia Lindley
Quercus dispersa	Q. dumosa Nuttall
West American Element	
Border-redwood Component	
Populus alexanderi	P. trichocarpa Torrey and Gray
*Populus pliotremuloides	P. tremuloides Michaux
Umbellularia salicifolia	U. californica Nuttall
Rocky Mountain Component	
Populus parce-dentata	P. acuminata Rydberg
*Populus pliotremuloides	P. tremuloides Michaux

*Species occurring in more than one component.

In an area 2 miles east of the fossil locality, at an elevation only 200 to 300 feet higher, a semiarid oak savanna of *Quercus douglasii* and *Q. wislizenii* forms an association which is characteristic of the lower slopes of the Sierra Nevada and extends north and south along the range for many miles. Such shrubs as *Arctostaphylos mariposa, Ceanothus cuneatus, Photinia arbutifolia, Quercus dumosa,* and *Ribes quercetorum,* which have equivalent fossil species in the

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Oakdale flora, make up a part of the chaparral in the oak country. Some of these, notably the gooseberry, are commonly scattered through the oak savanna. All these plants extend their ranges to lower levels on cooler slopes and in the river canyons, and live within a short distance of the fossil locality in the Stanislaus River valley. Here also are to be found *Salix lasiolepis* and *Umbellularia californica,* both of which have equivalent species in the Oakdale flora.

One of the modern equivalent Oakdale species, *Populus trichocarpa,* is not found along streams in the woodland on the lower Sierra Nevada slopes, but occurs in the Transition forest at higher elevations. Above the 1500-foot level in the region east of the fossil locality, it has been noted with *Pinus ponderosa, Quercus kelloggii,* and their regular associates. Members of this community descend to lower levels on cooler north slopes, thus overlapping the oak woodland and chaparral. In such situations *Populus trichocarpa* may occur in close proximity to many of the modern equivalent Oakdale species, but it is always associated with typical members of the Transition forest. In the south Coast Ranges and in southern California, on the other hand, *P. trichocarpa* is associated commonly with the modern equivalent Oakdale species that live also in the oak country of the lower Sierra Nevada, and in these areas it is found along streams considerably below the Transition forest zone. Since none of the members of the Transition zone forest, such as *Arbutus menziesii, Libocedrus decurrens, Lithocarpus densiflora, Pinus ponderosa, P. lambertiana, Quercus chrysolepis,* and *Q. kelloggii,* have fossil equivalents in the Oakdale flora, it is believed that the habitat of *Populus trichocarpa* in the south Coast Ranges and in southern California more nearly approaches the physical conditions suggested by the fossil assemblage.

Thirteen of the 16 modern equivalent Oakdale species live in southern California, where they comprise parts of its chaparral, woodland, and desert-border communities. *Ceanothus cuneatus, Photinia arbutifolia,* and *Quercus dumosa* are members of the chaparral, and the manzanita of the central Sierra Nevada, *Arctostaphylos mariposa,* is replaced here by the related *A. glauca* Lindley. The moister slopes and canyon bottoms at low to moderate elevations in this region regularly contain *Populus trichocarpa, Quercus wislizenii, Salix lasiolepis,* and *Umbellularia californica.* Although *Celtis reticulata, Mahonia fremontii,* and *Ribes quercetorum* are largely of desert-border occurrence in southern California, at Banning and Campo members of the chaparral and woodland formations extend downward along canyons to meet them.

One of the cottonwoods of the flora, *Populus parce-dentata,* finds its nearest living counterpart in the lance-leaf cottonwood (*P. acuminata*) of the Rocky Mountain area. In the southern parts of its range in southeastern Arizona and southern New Mexico, this cottonwood occurs in association with two of the Oakdale living equivalent plants no longer represented generically in the indigenous California flora. These species, *Robinia neo-mexicana* and *Sapindus drummondii,* are largely of woodland occurrence in this area. Among their associates having equivalent species in the Oakdale flora are *Celtis reticulata, Mahonia fremontii,* and *Ribes quercetorum.* One of the oaks of this area,

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Quercus turbinella Greene, is closely related to *Q. dumosa* of California, and the Californian *Q. wislizenii* finds an ecological counterpart in *Q. emoryi* Torrey. These plants not only occupy an ecological position essentially similar to that which they hold in the central Sierran foothills, but also are regular members of the woodland which is historically related to the California association (Axelrod, 1940*b*, p. 483).

The Pliocene aspen, *Populus pliotremuloides,* was recorded first by the writer in the semiarid Mount Eden flora of southern California (Axelrod, 1937). Its ecological interpretation in that area was puzzling because the modern species, *P. tremuloides,* occurs regularly in the higher mountains of the western states, where it forms colonies on the edges of marshes, lakes, and streams in areas usually considered as typical of the Upper Transition and Canadian life zones. The Mount Eden aspen was believed to have descended into that basin in deep canyons with cold air and water drainage. This interpretation was suggested by the fact that the living species has such a distribution in the more arid parts of its range in Oregon, Nevada, and California. Although the Oakdale aspen is considered to have had a similar occurrence, it nevertheless seems desirable to place on record some additional information pertaining to its modern and past distribution.

A particularly unusual habitat for *Populus tremuloides* was noted by Herbert L. Mason, during the summer of 1940, in the Hetch Hetchy region 40 miles east of the Oakdale locality. A grove of aspens was discovered at Swamp Lake on the edge of the north rim of the Tuolumne River gorge at an elevation of 5200 feet. This occurrence, which is about 2 miles west of Hetch Hetchy Dam, is noteworthy because the Tuolumne River canyon, over 2000 feet deep in this region, is sufficiently arid to permit the digger pine forest to extend into the area. All the south-facing slope of the canyon is occupied by this woodland community, whose associates include the following species having fossil equivalents in the Oakdale flora:

Ceanothus cuneatus	Quercus wislizenii
Photinia arbutifolia	Salix lasiolepis
Quercus dumosa	Umbellularia californica

These plants, as well as the digger pine, reach the top of the south canyon slope, where they are within ¼ mile of aspen.

This geographic proximity of plants belonging to the Upper Sonoran and Canadian zones, which are otherwise separated by the Transition forest in the Sierra Nevada, emphasizes the importance of relief and slope in controlling the distribution of vegetation. There is still another example of topographic control in this region which demands attention. Before Hetch Hetchy Dam was constructed, such high-montane conifers as *Abies magnifica* Murray, *Pinus contorta* var. *murrayana* Engelmann, and *Pinus monticola* Douglas, which normally live in this region at elevations above 6500 feet, descended along the Tuolumne River gorge to an altitude of 3500 feet (Herbert L. Mason, oral communication, September 1940). On the walls above the canyon floor there still are, in reversed

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order, the Transition forest and the Upper Sonoran digger pine community, which extends upward to 6000 feet. This inversion of three life zones has been due in large measure to the flow of cold air down the Tuolumne River gorge, which permits the establishment of upland species at lower levels. In such an epoch as the Pliocene, it cannot be doubted that topography played an equally important role in controlling the distribution of vegetation along the borders of mountainous areas where sediments were accumulating.

Evidence for such a distribution during Oakdale time is suggested by the character of the sediments in the adjacent region. At the immediate plant locality the deposits reveal the features of a broad flood plain. Two and 3 miles eastward, however, the nature of the stream channeling indicates that the river valleys in this area were narrow and deeply incised gorges, with arroyos of similar character. It may be suggested that aspen lived in this area, for it is sufficiently rare in the flora to indicate that it probably was situated at some distance from the immediate site of deposition. These deep arroyos along the edge of the Sierra Nevada block directly east of the fossil locality could readily afford the habitat suited for its establishment in this lowland area. It seems probable that aspen may also have extended its range for some distance from this area toward the fossil locality, in the same manner as *Populus tremuloides* extends out from the base of mountainous areas in Nevada today. (See pl. 32, fig. 2.)

From this discussion of the composition of the Oakdale flora, and its relationships to modern vegetation, it is evident that the flora was dominated by species whose nearest modern relatives contribute to three distinct habitats in semiarid regions: flood plain or riparian, savanna-woodland, and chaparral. The flood-plain assemblage at the Oakdale locality was composed of *Populus alexanderi, Robinia californica, Salix wildcatensis,* and *Sapindus oklahomensis,* with *Celtis kansana* and *Umbellularia salicifolia* present in subordinate numbers. Another member of this group is *Populus pliotremuloides,* which had a minor role in the flora.

The oak savanna community characterized the adjacent interfluvial areas. The dominant tree over this region was the live oak, *Quercus wislizenoides,* and associated with it was another xeric species, *Q.* cf. *douglasoides.* Judging from the habitats occupied by their nearest living equivalents, *Quercus wislizenii* and *Q. douglasii,* which have survived down to the present in the adjacent region, these oaks probably formed a savanna. This interpretation is suggested also by the presence of such grazing types as *Neohipparion, Pliohippus,* and *Pliauchenia* in the Oakdale fauna, which occurs slightly higher in the section. It is to be assumed also that the oaks formed dense woodlands on cooler slopes in the region, and that they probably occurred as well in the river valleys, in much the same manner as their living counterparts do today.

If the character of this predominant Oakdale environment is compared with present conditions near the fossil locality, as shown on plate 32, figure 1, there is ample reason for asserting that the general physiognomy of the vegetation has not changed greatly since Oakdale time. Only in the withdrawal of the oak

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community 2 or 3 miles eastward, and in its replacement by a dominant grassland, does there seem to be any notable change. Since there is evidence that oaks have been cleared from the grassland zone within historic time, this change in their distribution has no fundamental significance.

The more arid shrubs of the flora include *Arctostaphylos oakdalensis, Mahonia marginata, Photinia sonomensis, Quercus dispersa,* and *Ribes mehrtensis.* It is not to be doubted that they may have formed local brushy communities on drier slopes, and also inhabited the drier parts of the river valley with the oak community. The prominence of chaparral in the essentially contemporaneous Mulholland flora to the west (see chap. 5) suggests that a chaparral climax may have lived on exposed slopes bordering the Oakdale region. From a climatic standpoint it also seems likely that chaparral may have formed an important community in the region.

The probable amount of annual rainfall during Oakdale time may be estimated from an analysis of the rainfall requirements of living vegetation related to the fossil flora. It has been shown that a large number of the modern correlatives of the flora now survive in the foothill area directly east of the fossil locality. As gauged from climatic data for Oakdale,[2] where the average annual precipitation over a 42-year period is 14 inches, yearly rainfall in the oak-savanna region east of the fossil locality is considered to range from 18 to 20 inches. Over 80 per cent falls during the months from November to April, with July and August practically rainless. The black cottonwood (*Populus trichocarpa*), whose fossil equivalent (*P. alexanderi*) is one of the dominants of the Oakdale flora, does not occur in this foothill area where annual rainfall totals 18 to 20 inches, but first appears in the lower part of the Transition forest, where rainfall averages 35 inches yearly.[3] On the other hand, in the south Coast Ranges and in southern California it is associated with woodland and chaparral in areas where precipitation is as low as 18 to 20 inches. It would appear that a higher evaporation rate in the foothill region of the Sierra Nevada restricts *P. trichocarpa* to the Transition forest, where greater rainfall compensates for the high summer temperatures. In the south Coast Ranges conditions are more moderate, owing to the presence of summer fogs and moderating ocean breezes. As a result, the cottonwood can extend its range to levels below that of its Sierra Nevada Transition occurrence.

Populus alexanderi is considered to have lived at the immediate site of deposition because it is one of the most abundant species in the flora. Since its modern equivalent, *P. trichocarpa,* does not live with oak woodland vegetation in areas where precipitation is below 18 to 20 inches, it is believed that this figure approximates the minimum during Oakdale time. The presence of *Celtis, Mahonia,* and *Sapindus* in the flora suggests that rainfall probably was not much in excess of this figure. These plants are commonly of desert-border occurrence in the western United States, and although they may range upward into the woodland

[2] Oakdale is situated 7 miles west of the fossil locality and 50 feet lower in elevation.

[3] This figure represents average rainfall data for Sonora, San Andreas, and Mokelumne Hill, which are situated in the lower part of the Transition forest east of the fossil locality.

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community, they usually are not found in areas where rainfall greatly exceeds 20 inches. Since the annual rainfall at the fossil locality is now 14 to 15 inches, it is concluded that precipitation has been lowered approximately 5 inches since Oakdale time.

From the standpoint of rainfall distribution during this stage, the genera no longer found in California (*Robinia* and *Sapindus*), as well as the cottonwood having affinities in the Rocky Mountain region (*Populus parce-dentata*), assume significance because they now live in areas with summer precipitation. When they are considered together with the members of the East Asian and East American Elements that survived into later Pliocene time in the more moderate coastal areas of California, there is substantial evidence for summer as well as winter precipitation during the Oakdale stage.

Vegetation related to the fossil flora occurs in regions having high ranges of daily, seasonal, and yearly temperature. In Oakdale time summer temperatures appear to have been more moderate than those now prevailing in that region. This interpretation is suggested also by the ecological relationships of the black cottonwood (*Populus trichocarpa*), whose fossil equivalent (*P. alexanderi*) is one of the commonest species in the flora. It has already been pointed out that the modern species does not survive in the central Sierra Nevada foothills with the oaks and their associate shrubs that have modern equivalents in the flora, but is limited to higher elevations with the Transition yellow pine forest. Because none of the members of this community has been recorded in the Oakdale assemblage, it is believed that the association of *P. trichocarpa* with many of the modern representatives of the fossil flora in the south Coast Ranges and in southern California more nearly represents Oakdale conditions. Judging from published temperature charts for California, the distribution of black cottonwood in areas of low rainfall (18 to 20 inches) is apparently limited by high summer temperatures. In general it seems to be controlled by an average July maximum not exceeding 85° F., and by extremes of summer temperature not greater than 110° F. Data for the fossil locality, as indicated by meteorological records for Oakdale, 7 miles west, show an average July maximum of 95.8° F. This is fully 10° higher than the maxima now found in the range of black cottonwood in regions of limited rainfall. The extreme summer temperature for Oakdale is 114° F., or 4° higher than extremes occurring within the distribution of the species. These data suggest that there has been a trend to higher summer temperatures in the central Sierra Nevada foothills since Oakdale time.

The general physical conditions suggested by the preceding analysis of the flora may be summarized as follows:

1. The Oakdale flora represents woody vegetation that lived in the lowest foothill region of the central Sierra Nevada at an elevation of approximately 200 feet. It is preserved in coarse, fluviatile, andesitic sands derived from eruptions in the high Sierra Nevada a few tens of miles distant.

2. The flora includes riparian species of cottonwood (*Populus*), locust (*Robinia*), willow (*Salix*), and soapberry (*Sapindus*), with such species as hackberry (*Celtis*) and California laurel (*Umbellularia*) occurring in lesser

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numbers. Aspen (*Populus*) lived in narrow canyons in the near-by foothill area, and extended its range toward the fossil locality. The adjacent interfluvial areas were characterized by an oak savanna, with associates of barberry (*Mahonia*), scrub oak (*Quercus*), buckbrush (*Ceanothus*), toyon (*Photinia*), and manzanita (*Arctostaphylos*). These plants occurred also in the drier parts of the river valley, and the shrubs may have formed a chaparral climax on drier exposed slopes.

3. The climate at this time was characterized by an annual rainfall of 18 to 20 inches. Although it was distributed during the summer and winter months, the total summer precipitation may well have been less than that during the winter. Summer temperatures were considerably lower than those now prevailing in the lower Sierran foothills. This may have been due to occasional summer fogs and moderating ocean breezes, which were able to extend into this region since the Coast Ranges at the west were then a comparatively low barrier.

The climate in the central Sierran foothill area must have been gradually altered as the Coast Ranges were elevated during late Cenozoic time. The building up of this mountain barrier had a twofold effect on the climate of the lower foothill region. In the first place, the rain shadow cast over the inland area was sufficient to produce a lowering of rainfall amounting to about 5 inches annually. This has resulted in the restriction of the oak savanna community toward the east, where precipitation is greater than in the grassland area surrounding the fossil locality. The second effect was the formation of an effective barrier to the summer fogs and moderating ocean breezes which are considered to have extended into the area about as they do today in the south Coast Ranges. The disappearance of these ameliorating conditions seems to have been responsible in large measure for the restriction of *Populus alexanderi* (*P. trichocarpa*) upward into the yellow pine forest. A larger Oakdale collection might show that certain of its regular associates in the Sierra Nevada today, such as *Acer macrophyllum, Arbutus menziesii,* and *Quercus kelloggii,* had a limited distribution in the lower central Sierran foothills during Oakdale time. Whereas these plants are largely restricted to the Transition forest in the Sierra Nevada, it is significant that they also survive with woodland vegetation in the Coast Ranges, where rainfall is lower, but where summer temperatures are more moderate and evaporation is lower. A discussion of this distribution is included in the preceding chapter, on the Mulholland flora.

Age of the Flora

Tertiary floras have undergone marked changes in distribution and composition in response to the compulsion of climatic change (Chaney, 1940). By taking into account the geographic position of a flora, and by analyzing its floristic elements from the standpoint of modification in response to the general trend to aridity in the western United States during the later Tertiary, age may be gauged rather accurately.

The nearest flora for comparison with the Oakdale is the transitional Mio-Pliocene Table Mountain (chap. 3), which contains elements derived from the Arcto-Tertiary and Madro-Tertiary Floras. Members of the Arcto-Tertiary

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Flora are dominant and represent three distinctive groups: (1) the East American, which includes *Berchemia, Carya,* and *Magnolia,* (2) the East Asian, which includes *Rhododendron* and *Ulmus,* and (3) the West American, which includes *Arbutus, Philadelphus, Pinus,* and *Umbellularia* of the Border-redwood Component. All these plants are considered to have occupied the moister slopes and lowland valleys adjacent to the Table Mountain site of deposition. Exposed areas were inhabited by such members of the semiarid Southwest American Element as *Celtis kansana, Cercocarpus antiquus, Forestiera buchananensis, Quercus convexa, Q. dispersa,* and *Robinia californica.* Since members of this group are sufficiently abundant to comprise over a third of the recorded flora, it would appear that this semiarid element was diversified and well developed in drier areas bordering sites of deposition.

Whereas the Table Mountain flora represents vegetation from an altitude of approximately 500 feet, the Oakdale flora lived within 200 feet of sea level, 25 miles to the west. It must be emphasized that vegetation in areas of low to moderate rainfall rapidly becomes more mesic with a slight rise in elevation, and hence its composition changes greatly. Thus it is to be expected that contemporaneous vegetation at elevations below the Table Mountain locality would be more xeric in aspect, and that genera of mesic types would hold a subordinate position in the flora. One of the salient facts regarding the Oakdale flora is that it does not contain any of the mesic species which dominated the river banks and lowland valleys of the central Sierra Nevada during Table Mountain time.[4] In addition, certain of the more hardy members of the East Asian and East American Elements apparently did not persist into the Oakdale stage in the lower foothill area of the central Sierra Nevada. Furthermore, members of the Arcto-Tertiary Flora whose nearest descendants have survived to form part of the Sierra-Cascade forest in the Sierra Nevada are not represented in the Oakdale collections.

The fact that none of the members of these groups have been encountered at Oakdale indicates a degree of climatic and floristic change in the lower Sierran foothills between Table Mountain and Oakdale time sufficient to suggest an age later than Lower Pliocene. The elimination of these mesic northern groups from the lower slopes of the range by this time seems to have been due to the rising Coast Range barrier at the west, casting a rain shadow over the lower slopes of the area, as well as to the general trend toward aridity in the western United States during the later Tertiary. If members of the East American and East Asian Elements survived in the central Sierra Nevada during Oakdale time, they probably lived at higher elevations, where rainfall was greater and temperatures were more moderate. From such situations their leaves and other structures would have but slight opportunity of entering the Oakdale deposit, which was accumulating at the foot of the range. If the Oakdale flora

[4] Condit has suggested that such plants as *Magnolia californica, Persea pseudo-carolinensis,* and *Platanus dissecta* may have extended through the Sierran foothill area and across the present Great Valley into the coastal region (chap. 3, p. 67).

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were of Lower Pliocene age, it might be expected not only to contain certain members of the Sierra-Cascade Component, but to have also a limited representation of the East Asian and East American Elements.

The post-Lower Pliocene age of the Oakdale assemblage is suggested also by the manner in which members of the Southwest American Element had gradually assumed dominance over the mesic northern forest in the central Sierran region. By the beginning of Pliocene time woodland and chaparral vegetation had an important role on the lower slopes of the range. A large number of Table Mountain species may be referred to a Middle Tertiary north Mexican origin, and three of these, *Celtis kansana, Quercus dispersa,* and *Robinia californica,* survived into the Oakdale flora. In addition, the Oakdale has southern species of *Arctostaphylos, Mahonia, Quercus,* and *Sapindus,* all of which might be expected to occur at Table Mountain. The trend to aridity in this region between Table Mountain and Oakdale time represents a change from Arid Transition–Upper Sonoran to overwhelmingly Upper Sonoran conditions. Involving the elimination of the mesic elements from the lower foothill area, this change seems of sufficient magnitude to indicate that the flora is of Middle Pliocene age.

A comparison with the Mulholland flora from the eastern Berkeley Hills also suggests that the flora is Middle Pliocene in age. The following 9 out of 16 Oakdale species occur in the early Middle Pliocene Mulholland:

Celtis kansana	Quercus wislizenoides
Mahonia marginata	Salix wildcatensis
Photinia sonomensis	Sapindus oklahomensis
Populus alexanderi	Umbellularia salicifolia
Populus parce-dentata	

Both floras are characterized by an oak savanna-woodland and its regular riparian and chaparral associates. It is to be noted that the same oak, *Quercus wislizenoides,* dominates both floras. Another feature common to the two floras is the relatively large development of the Southwest American Element. The fact that both floras are dominated by woodland vegetation suggests that they are not greatly different in age. The early Middle Pliocene Mulholland flora differs from the Oakdale, however, in that it contains members of the Border-redwood Component (*Alnus, Arbutus, Cornus, Fraxinus, Prunus, Rhus*), in addition to certain members of the East American and East Asian Elements (*Berchemia, Nyssa, Quercus*). The larger specific representation of these mesic groups at Mulholland is to be attributed probably to the coastal position of that flora. It has already been pointed out that they could have survived in the central Sierra Nevada during Oakdale time only if they lived in more mesic upland areas away from accumulating lowland sediments. A flora of essentially Mulholland composition in the Oakdale region, that is, a flora containing a dominant Oak woodland Component with a subordinate Border-redwood Component and East American and East Asian relicts, would clearly be older than

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the Oakdale. In view of the complete absence of these mesic types in the Oakdale, it is considered to be younger than the Mulholland, and to belong more nearly to the middle than to the earliest part of the Middle Pliocene.

This age reference finds support in the occurrence of the Middle Pliocene Oakdale fauna near by (Stirton and Goeriz, 1942). The andesitic sediments at the plant locality grade upward into finer tuffaceous deposits. These occur about 125 feet stratigraphically above the flora and have been traced northwesterly 2 to 3 miles to the Oakdale faunal localities. The stratigraphic separation of the flora and fauna, and the fact that the intervening sediments show that erosion was taking place during deposition, indicate that the Oakdale fauna and flora are not exactly contemporaneous. The flora is considered to be slightly older than the fauna, perhaps belonging to the earlier rather than to the later half of the Hemphillian stage.

Summary

The Oakdale flora is preserved in coarse andesitic sediments which were laid down in the lowest foothill region of the central Sierra Nevada. The flora, which largely represents a flood-plain community living in a region dominated by an oak savanna-woodland, is related to modern vegetation in the adjacent Sierra Nevada, the inner south Coast Ranges of California, and southern California, and also contains plants whose nearest relatives are now found in southern Arizona.

The climate during Oakdale time differed from present conditions in that region in having a higher rainfall, summer as well as winter precipitation, and occasional moderating fogs and ocean breezes which resulted in cooler summers.

On the basis of its floristic character and its relationships to floras of known age in the near-by region, the Oakdale flora is considered to be of Middle Pliocene age, an interpretation in harmony with vertebrate evidence.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class ANGIOSPERMAE
Subclass DICOTYLEDONES
Family SALICACEAE

Populus alexanderi Dorf

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, figs. 10, 11 (not fig. 9, which is *P. prefremontii* Dorf); pl. 7, figs. 2, 3 (not fig. 1, which is *P. prefremontii*), 1930.

Condit, Carnegie Inst. Wash. Pub. 553, p. 40, 1944 (see synonymy).

This characteristic Pliocene cottonwood, which is related to the modern *Populus trichocarpa* Torrey and Gray, is one of the commonest species in the Oakdale flora.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1704, 1705, 1706, 1707.

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Populus parce-dentata (Lesquereux) Axelrod

(Plate 33, figure 1)

Populus parce-dentata (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 129–130, pl. 27, figs. 1, 3, 1944.

Two characteristic leaves representing this species have been encountered in the Oakdale flora. Among modern plants, *Populus parce-dentata* is related most closely to *P. acuminata* Rydberg, which is distributed through the Rocky Mountain region from Alberta into southeastern Arizona and southern New Mexico. In this latter area it occurs with species of *Celtis, Mahonia, Robinia,* and *Sapindus* which have fossil equivalents in the Oakdale flora.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1702; no. 1703.

Populus pliotremuloides Axelrod

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 169–170, pl. 4, figs. 1–3, 1938.

Several typical ovate leaves of *Populus pliotremuloides* are represented in the Oakdale flora. The ecological significance of this small-leafed aspen, which is now known to have had a wide distribution in later Tertiary time, has been discussed on pages 153 to 154.

Populus pliotremuloides has been recorded in several floras floristically similar to the Oakdale. At Mount Eden (Axelrod, 1937) it occurs with 4 species which are represented in the Oakdale flora, *Ceanothus precuneatus, Quercus douglasoides, Sapindus oklahomensis,* and *Salix wildcatensis,* and the Mount Eden manzanita, *Arctostaphylos preglauca,* is related to *A. oakdalensis.* In the Lower Pliocene Esmeralda (Axelrod, 1940*a*) and Truckee floras (Axelrod, unpublished) of western Nevada, aspen has been recorded with the following species also found in the Oakdale: *Ceanothus precuneatus, Celtis kansana, Populus alexanderi,* and *Quercus wislizenoides.* There is also a close relationship between *Arctostaphylos* of the Esmeralda and Oakdale floras. Aside from these specific relationships, it is even more critical that all three floras represent woodland vegetation. Aspen has been recorded also in the early Middle Miocene Tehachapi flora of the Mohave Desert (Axelrod, 1939), which represents a part of the Madro-Tertiary Flora that contributed many genera and species to the Pliocene floras in the western United States. These Miocene and Pliocene occurrences of aspen lend considerable weight to the belief that it may have been a regular member of the southern woodland flora. Since the leaves of the fossil species cannot be differentiated from those produced by *Populus tremuloides* Michaux in the drier parts of its range in the western United States, it may be suggested that the distinction is purely physiological. The modern aspen of the Great Basin area which ranges into the sagebrush country, and the Swamp Lake record discussed on page 153, seem to represent most closely the physical conditions suggested by *Populus pliotremuloides.*

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 1708, 1709.

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Salix wildcatensis Axelrod

Salix wildcatensis Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

Several fragments of large willow leaves with entire margins and irregular secondaries are identified as belonging to this species, which resembles the modern *Salix lasiolepis* Bentham of California.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1726.

Family FAGACEAE

Quercus dispersa (Lesquereux) Axelrod

Quercus dispersa (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 97–98, pl. 7, figs. 8, 9, 1939.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 76–77, 1944 (see synonymy).

A single but well preserved scrub-oak leaf is referred to this species, which shows a close relationship to the living *Quercus dumosa* Nuttall of California. The latter, which occurs near the fossil locality at the present time, has a wide distribution in California, ranging from the northern Great Valley southward into Baja California. It is a regular component of the chaparral, and, like many of the species of that community, appears to have had a southern origin during the Middle Tertiary (Axelrod, 1939, pp. 64–65).

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1710.

Quercus cf. **douglasoides** Axelrod

Quercus douglasoides Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 198–199, pl. 37, figs. 7–10, 1944 (see synonymy and discussion).

Part of an oak leaf in the flora seems referable to this species, which represents the later Tertiary equivalent of the modern blue oak, *Quercus douglasii* Hooker and Arnott, of California.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1711.

Quercus wislizenoides Axelrod

(Plate 33, figures 2, 5)

Quercus wislizenoides Axelrod, Carnegie Inst. Wash. Pub. 553, p. 136, pl. 29, figs. 4–9, 1944 (see synonymy).

This oak is one of the dominants of the flora, and its nearest related modern equivalent, *Quercus wislizenii* A. DeCandolle, still survives in the vicinity of the fossil locality as an important component of the savanna.

In addition to its central California occurrences during the Pliocene in the Anaverde, Mulholland, Petaluma, and San Joaquin floras, *Q. wislizenoides* has recently been recorded in the Truckee formation of western Nevada. There now appears to be sufficient evidence to indicate that this species characterized the woodland of central California in Middle Pliocene time, and the woodland of the central Great Basin during the Lower Pliocene.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1712, 1713; nos. 1714, 1715, 1716, and possibly 1717.

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Family ULMACEAE

Celtis kansana Chaney and Elias

Celtis kansana Chaney and Elias, Carnegie Inst. Wash. Pub. 476, I, pp. 38–39, pl. 5, figs. 1–5, 1936.

Condit, Carnegie Inst. Wash. Pub. 553, p. 77, pl. 14, fig. 4, 1944 (see synonymy).

Celtis kansana is represented in the flora by an impression of a fruit showing the characteristic surface markings. A mid portion of a leaf blade may also represent this species. Hackberry has been recorded in the Table Mountain flora of the adjacent region, in the Mulholland flora of west-central California, and in other Pliocene floras. The nearest occurrence of its modern descendant, *Celtis reticulata* Torrey, to these central California localities is in the southern Sierra Nevada.

Collections. U. C. Mus. Pal., Paleobot. Ser., nos. 1718, 1719.

Family BERBERIDACEAE

Mahonia marginata (Lesquereux) Arnold

(Plate 33, figure 6)

Mahonia marginata (Lesquereux) Arnold, Contr. Mus. Paleontol. Univ. Mich., vol. 5, no. 4, pp. 64–65, 1936.

Axelrod, Carnegie Inst. Wash. Pub. 553, p. 137, 1944 (see synonymy).

Leaflets of a barberry showing close relationship to the modern *Mahonia fremontii* (Torrey) Fedde are abundantly preserved in the Oakdale flora. In addition to its later Tertiary occurrences at Creede, Mulholland, and Esmeralda, this species has been recorded also at Florissant and more recently at Mint Canyon. It is probable that the slender leaflet recorded as *M. mohavensis* from the Tehachapi flora (Axelrod, 1939) represents only a variation of this species.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 1720; nos. 1721, 1722.

Family LAURACEAE

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939 (see synonymy).

The terminal part of a coriaceous leaf, with a slightly emarginate tip, and with straight secondaries departing at moderate angles and then looping sharply upward within the blade, is clearly assignable to this common middle and later Tertiary species. Its nearest modern relative, *Umbellularia californica* Nuttall, has survived down to the present in the Stanislaus River valley directly east of the Oakdale locality.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1725.

Family SAXIFRAGACEAE

Ribes mehrtensis new species

(Plate 33, figures 3, 7)

Description. Leaves broadly rounded to oval, 5-lobed and pedate; one leaf 1.2 cm. wide and 8.0 mm. long, another 8.0 mm. wide and 1.0 cm. long (estimated); petiole

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of medium texture, 5.0 mm. long, attached to twig; primaries thin and straight, alternate secondaries supplying subsidiary lobes; tertiaries not preserved; margin crenate-entire; texture thin.

Discussion. These leaves of gooseberry resemble those produced by several living species, but they show closest relationship to those of the modern *Ribes quercetorum* Greene. This semiarid species ranges from the central Sierra Nevada and inner south Coast Ranges into southern California, and reappears in south-central Arizona. Judged by the character of its distribution, and the nature of its associates in the Oakdale flora, this species represents a member of the Madro-Tertiary Flora.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 1723, 1724.

Family ROSACEAE

Photinia sonomensis Axelrod

Photinia sonomensis Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 139–140, 1944 (see synonymy and discussion).

The mid portion of a leaf showing the essential features of this species—conspicuous intersecondaries, sharp marginal teeth, wavering and subcamptodrome secondaries, thick and coriaceous texture—is represented in the Oakdale collection. Its nearest modern relative, *Photinia arbutifolia* Lindley, still persists in the general vicinity of the fossil locality.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1735.

Family LEGUMINOSAE

Robinia californica Axelrod

(Plate 33, figure 4)

Robinia californica Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 114–115, pl. 9, figs. 10–12, 1939.

Condit, Carnegie Inst. Wash. Pub. 553, p. 84, pl. 17, figs. 4, 5, 1944 (see synonymy).

Several leaflets of leguminous character are referred to this species, which is considered to be related to the modern *Robinia neo-mexicana* Gray of the southwestern United States and northern Mexico. *Robinia californica* is another member of the semiarid Southwest American Element that spread northward into central California during later Tertiary time, and was restricted southward later in that stage in response to the disappearance of summer precipitation.

In addition to its Oakdale occurrence, it has been recorded in the near-by Table Mountain flora and the Tehachapi flora, and has also been collected recently in the Mint Canyon flora of southern California.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 1727, 1727*a* (counterpart); nos. 1728, 1729.

Family SAPINDACEAE

Sapindus oklahomensis Berry

(Plate 33, figures 8, 9)

Sapindus oklahomensis Berry, Proc. U. S. Nat. Mus., vol. 54, pp. 632–633, pl. 95, figs. 1, 2, 1918.

Axelrod, Carnegie Inst. Wash. Pub. 553, p. 142, pl. 31, figs. 1, 2, 1944 (see synonymy).

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Leaflets of this species form one of the dominants of the flora. *Sapindus oklahomensis,* which is related to the modern *S. drummondii* Hooker and Arnott of the southwestern United States and northern Mexico, is a common member of the floodplain vegetation and often extends out into typical desert habitats.

In addition to its Oakdale occurrence, *Sapindus oklahomensis* has been recorded in the Mulholland, Mount Eden, and San Joaquin floras of California. A leaf fragment in the Esmeralda collections at the U. S. National Museum may also be referable to this species.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1730, 1730*a* (counterpart), 1731; no. 1732.

Family RHAMNACEAE

Ceanothus precuneatus Axelrod

Ceanothus precuneatus Axelrod, Carnegie Inst. Wash. Pub. 516, p. 120, pl. 11, fig. 7, 1939.

Two leaf impressions, one of which has since been misplaced, identify this species in the Oakdale flora. The fossil species is related to the modern *Ceanothus cuneatus* Nuttall, a species which has survived down to the present near the fossil locality.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1733.

Family ERICACEAE

Arctostaphylos oakdalensis new species

(Plate 33, figure 10)

Description. Leaf oval, slightly asymmetrical; 3.5 cm. long and 2.8 cm. wide; heavy petiole 1.3 cm. long; midrib heavy and straight; alternate secondaries diverging at angles of from 50° in the lower part of the blade to as low as 10° in the upper part, secondaries wavering and bifurcating in the outer part of the blade; tertiaries obscure but apparently irregular; margin entire; texture heavy and coriaceous.

Discussion. This leaf impression is clearly that of a manzanita. Although it is fully realized that leaf variation within a single living species of *Arctostaphylos* is often sufficient to overlap into several others, this Oakdale specimen seems relatively distinct. Among modern species it shows closest relationship to *A. mariposa* Dudley of the central Sierran region. The leaves of the closely related *A. glauca* Lindley may also resemble this species, but the fossil more nearly resembles the normal variation of the *mariposa* type.

Further collections may show that the Esmeralda species, which was referred tentatively to *A. preglauca* Axelrod, is more properly assignable to *A. oakdalensis.*

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1734.

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PLATES 32, 33

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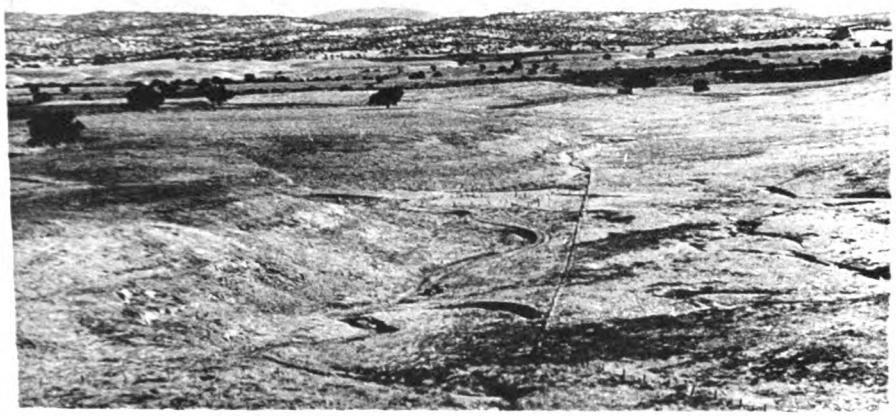

FIG. 1. The Oakdale locality (P3628), on the slope in the lower left corner. The general physiognomy of the near-by vegetation has not changed greatly since Middle Pliocene time.

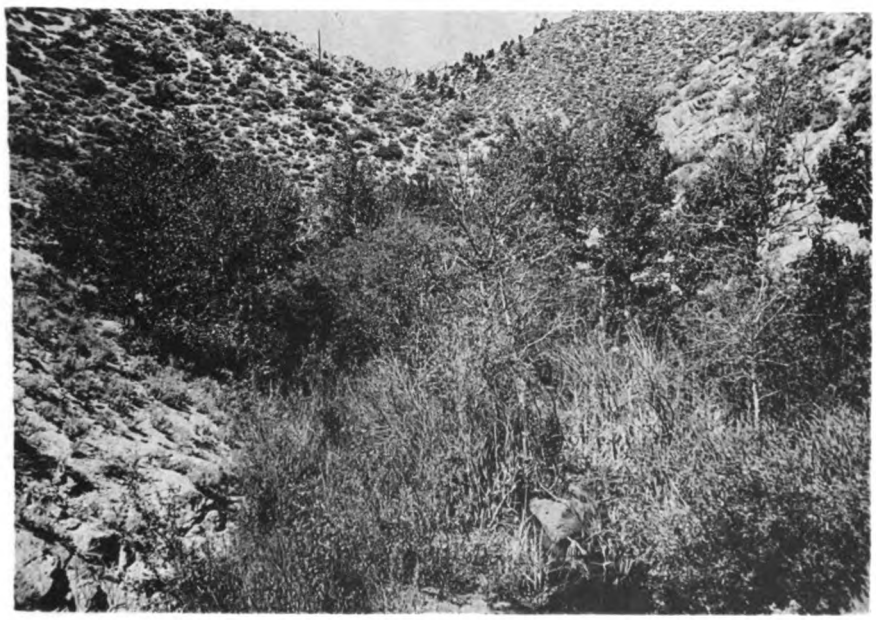

FIG. 2. *Populus tremuloides* in the sagebrush country of Nevada. A similar topographic control seems to have been in operation during the later Tertiary.

OAKDALE LOCALITY AND RELATED VEGETATION

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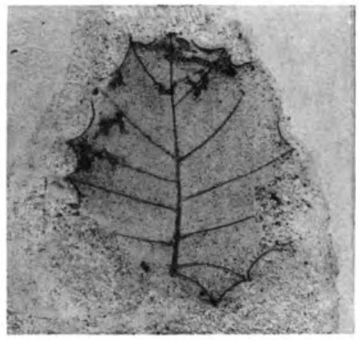

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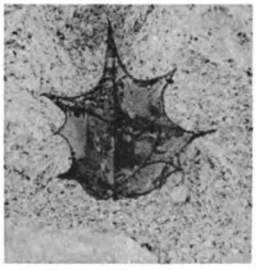

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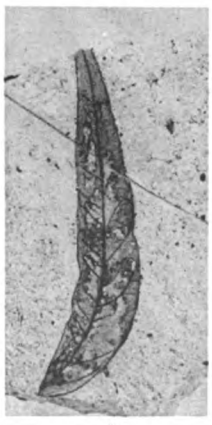

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PLATE 33

Oakdale fossils

PAGE

Fig. 1. *Populus parce-dentata* (Lesquereux) Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1702 161

Figs. 2, 5. *Quercus wislizenoides* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1713, 1712 162

Figs. 3, 7. *Ribes mehrtensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1723, 1724 163

Fig. 4. *Robinia californica* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1727 164

Fig. 6. *Mahonia marginata* (Lesquereux) Arnold. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1720 163

Figs. 8, 9. *Sapindus oklahomensis* Berry. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1730, 1731 164

Fig. 10. *Arctostaphylos oakdalensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1734 165

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7

The Sonoma Flora

DANIEL I. AXELROD

Introduction

New information regarding most of the Pliocene formations of California from which Dorf (1930) made his paleobotanical collections has become available during the past decade. Some of the floras are now known to be in different formations from those to which they were originally assigned, and the ages of others have been revised. It has been determined also that in west-central California, Pliocene climate involves more than the originally suggested trend from relatively hot and dry conditions early in the epoch to a cooler and moister climate later in the stage. There now is sufficient evidence to indicate that Lower Pliocene time in this region was largely a continuation of Miocene conditions, modified to some extent by the general trend to aridity. The Middle Pliocene was the driest part of the epoch in west-central California, and was characterized by biseasonal rainfall distribution. Upper Pliocene time shows a trend to conditions cooler and more moist than those now existing at Upper Pliocene localities, and the elimination of summer rains. In other words, the trend from a warm and dry to a cooler and moister climate recognized by Dorf is now considered to have characterized only Middle and Upper Pliocene times in west-central California.

In view of this revision of the climatic basis for evaluating the ages of Pliocene floras in west-central California, it seems evident that some of the floras may have an age younger than that originally assigned to them. Most notable among these are the Sonoma, Petaluma,[1] and Wildcat floras north of San Francisco Bay, all of which have been referred to the Lower Pliocene. If they have been interpreted properly, and if the original collections are representative of the respective floras, it follows that all of them must be of Middle or Upper Pliocene age, for, as described, they all suggest conditions drier and warmer than are found in those regions today.

With the recent discovery of *Trapa americana* Knowlton in the Sonoma tuffs by Thomas Robbins, a student in the Department of Botany at the University of California, it seemed desirable to make further collections in the formation. New material would aid in testing the theory of a somewhat younger age for the Sonoma flora, and in determining whether any other plants in addition to *Trapa,* heretofore considered limited to the Miocene in the western United States, could be found in the sediments. With assistance from Robert E. Smith, the writer obtained additional material from two localities in the Sonoma forma-

[1] This was recorded as the Merced flora by Dorf (1930), and is discussed on pages 186 to 187 of this chapter.

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tion which have already been described by Dorf. The largest and most important collection is from Neer's Hill (locality 154), directly north of Santa Rosa. The second comes from the leaf-bearing horizons in the Petrified Forest (locality 150), 12 miles northeast of Santa Rosa. It was not possible to make a new collection at Matanzas Creek (locality 152), but Dorf has turned over his duplicate collections from this locality, and from the Petrified Forest, to the writer for further study.

Geologic Occurrence

The geologic occurrence of the plant localities in the Sonoma formation has been discussed in detail by Dorf (1930, pp. 7–13), so it seems necessary to indicate only the nature of the recent discoveries in the region which have a bearing on the formation.

The Sonoma formation represents an accumulation of several thousand feet of volcanics which extend over a large part of Napa County and overlap into the adjacent parts of Sonoma and Lake counties. On the western borders of Santa Rosa and Petaluma valleys, tuffaceous beds belonging to the Sonoma are intercalated in marine sediments which have been interpreted as the Merced (Dickerson, 1922; Johnson, 1934). Collections of marine invertebrates from these tuffs were correlated originally by Dickerson with the Lower Merced, and considered to be essentially equivalent to the Lower Pliocene Jacalitos of the Coalinga district. More recently, Johnson (1934) submitted a collection of invertebrates to C. W. Merriam, who reports them to be not older than Middle Pliocene. Although no suggestion was made as to the upper age limit of the fauna, it should be pointed out that Clark has expressed the opinion (*in* Dorf, 1930, p. 16) that part of the Merced might represent the later Pliocene, and perhaps some of the Pleistocene. Grant and Gale (1931, p. 55) have indicated that the Upper Merced may be correlated with the early Pleistocene of southern California, and have suggested a correlation (*ibid.*, table, p. 61) of the remainder of the Merced with the *Pecten coalingensis* zone of the Coalinga district. This zone is now considered to be in the San Joaquin formation and is regarded as Upper Pliocene in age. Charles E. Weaver, who has recently completed a geological survey of the Santa Rosa and adjacent quadrangles, has expressed the opinion (written communication, December 1940) that the Merced invertebrate fauna will require a more detailed faunal analysis before a definite position for those beds can be established in the Pliocene sequence of the Coast Ranges of California. Since Weaver considers that the Sonoma is probably Upper Pliocene in age, it follows that the part of the Merced on the western border of Santa Rosa Valley containing intercalated Sonoma tuffs may also belong to the Upper Pliocene.

The Sonoma overlies the Petaluma formation with marked angular discordance in the region southeast of Santa Rosa. The *Neohipparion gidleyi* horizon, which for many years was considered to be in the basal part of the Sonoma, is now known to be in the upper part of the Petaluma (Morse and Bailey, 1935). On the basis of a comparison with other Neohipparions in the

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western United States, Stirton (1939*a*, p. 393) is of the opinion that "the characters of *N. gidleyi* are . . . sufficiently advanced over those of the Middle Pliocene Neohipparions to warrant recognition of that species as belonging to an Upper Pliocene fauna. Our present knowledge of the progression of North American Equidae does not warrant considering this species older than late Middle Pliocene." Since the Sonoma formation unconformably overlies this vertebrate horizon, it would appear that the Sonoma is not older than Upper Pliocene. As noted above, however, the previously described Sonoma flora as interpreted from the climatic trend now known for the Pliocene of west-central California represents the Middle Pliocene. It has seemed desirable to obtain additional plant material from the Sonoma, since this problem arises from the conflicting evidence of its age position.

Composition and Physical Indications

The Sonoma flora listed below includes all species which have been collected from the Petrified Forest (loc. 150), Matanzas Creek (loc. 152), and Neer's Hill (loc. 154) localities. The complete flora includes 44 species, namely, 1 pteridophyte, 6 conifers, and 37 angiosperms. Thirty-seven of the 44 species have been reported previously in Miocene and Pliocene floras in the western United States, 9 are described as new, 1 (*Castanopsis*) is given a new name, 1 (*Lithocarpus*) is a new combination, and 2 others (*Ceanothus* and *Rhododendron*), which are not represented by sufficient material to warrant description as new species, are referred to genera only.

Systematic List of Species

Pteridophyta
- Filicales
  - Polypodiaceae
    - Pteris calabazensis Dorf

Spermatophyta
- Gymnospermae
  - Coniferales
    - Pinaceae
      - Abies sonomensis new species
      - Picea sonomensis new species
      - Pseudotsuga sonomensis Dorf
      - Tsuga sonomensis new species
    - Taxodiaceae
      - Sequoia langsdorfii (Brongniart) Heer
    - Cupressaceae
      - Cupressus sonomensis new species
- Angiospermae
  - Monocotyledones
    - Liliales
      - Liliaceae
        - Smilax sp. Dorf

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- Dicotyledones
  - Salicales
    - Salicaceae
      - Populus alexanderi Dorf
      - Populus pliotremuloides Axelrod
      - Salix boisiensis H. V. Smith
      - Salix wildcatensis Axelrod
  - Myricales
    - Myricaceae
      - Myrica sonomensis new species
  - Fagales
    - Betulaceae
      - Alnus merriami Dorf
      - Alnus rubroides new species
    - Fagaceae
      - Castanea pliocenica new species
      - Castanopsis sonomensis new name
      - Lithocarpus klamathensis (MacGinitie) new combination
      - Quercus bockéei Dorf
      - Quercus convexa Lesquereux
      - Quercus declinata Dorf
      - Quercus douglasoides new species
      - Quercus hannibali Dorf
      - Quercus lakevillensis Dorf
  - Urticales
    - Ulmaceae
      - Ulmus cf. tanneri Chaney
  - Ranales
    - Nymphaeaceae
      - Nymphaeites nevadensis (Knowlton) Brown
    - Berberidaceae
      - Mahonia hollicki (Dorf) Arnold
      - Mahonia prelanceolata Condit
      - Mahonia simplex (Newberry) Arnold
    - Lauraceae
      - Persea coalingensis (Dorf) Axelrod
      - Umbellularia salicifolia (Lesquereux) Axelrod
  - Rosales
    - Platanaceae
      - Platanus paucidentata Dorf
    - Rosaceae
      - Photinia sonomensis Axelrod
    - Leguminosae
      - Amorpha condoni Chaney
  - Sapindales
    - Aquifoliaceae
      - Ilex sonomensis Dorf
  - Rhamnales
    - Rhamnaceae
      - Ceanothus precuneatus Axelrod

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Ceanothus sp.
Rhamnus idahoensis Brown
Myrtales
Hydrocaryaceae
Trapa americana Knowlton
Umbellales
Cornaceae
Garrya masoni Dorf
Ericales
Ericaceae
Rhododendron sp.
Vaccinium sonomensis new species
Gentianales
Oleaceae
Fraxinus caudata Dorf
Rubiales
Caprifoliaceae
Symphoricarpos salmonensis Brown

The local distribution of the 44 species at the three localities is shown in table 16. The following species reported by Dorf from these horizons were not encountered in the present study, but it has seemed desirable to include them in the list, where they are indicated by an o: Matanzas Creek: *Alnus merriami, Ilex sonomensis, Garrya masoni;* Neer's Hill: *Ilex sonomensis, Populus alexanderi.* Table 16 shows that only 5 species, *Castanopsis sonomensis, Ilex sonomensis, Garrya masoni, Persea coalingensis,* and *Sequoia langsdorfii,* have been encountered at all three localities, 13 occur at two localities, and 26 are limited to one. It is to be expected that these relationships will be altered somewhat as new collections are made at the smaller localities. Nevertheless, some of the differences probably are to be attributed to habitat: the Neer's Hill florule was laid down essentially at sea level, but the Petrified Forest accumulated several hundred feet higher and farther inland.

The Sonoma flora is represented by slightly more than 600 specimens, but owing to the large number of species this is considered insufficient to make an accurate statement on the relative abundance of the various species. Judging from the data presented by Dorf (1930, pp. 32–33), supplemented by the recent collections, the following species are most abundant at the three localities:

Neer's Hill	*Petrified Forest*	*Matanzas Creek*
Abies sonomensis	Ilex sonomensis	Platanus paucidentata
Persea coalingensis	Persea coalingensis	Populus alexanderi
Quercus douglasoides	Pseudotsuga sonomensis	Populus pliotremuloides
Quercus lakevillensis	Quercus bockéei	
Sequoia langsdorfii	Quercus lakevillensis	
Trapa americana	Sequoia langsdorfii	

None of the remaining species is represented by more than 10 specimens.

In order to interpret the physical conditions under which the Sonoma flora

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TABLE 16

LOCAL DISTRIBUTION OF THE SONOMA FLORA

Species	*Petrified Forest*	*Matanzas Creek*	*Neer's Hill*
Abies sonomensis	x	..	x
Alnus merriami	..	o	x
Alnus rubroides	..	..	x
Amorpha condoni	..	..	x
Castanea pliocenica	..	..	x
Castanopsis sonomensis	x	x	x
Ceanothus precuneatus	..	..	x
Ceanothus sp.	x	..	..
Cupressus sonomensis	..	..	x
Fraxinus caudata	..	x	x
Garrya masoni	x	o	x
Ilex sonomensis	x	o	o
Lithocarpus klamathensis	..	..	x
Mahonia hollicki	x	..	..
Mahonia prelanceolata	..	..	x
Mahonia simplex	..	..	x
Myrica sonomensis	x	..	x
Nymphaeites nevadensis	..	..	x
Persea coalingensis	x	x	x
Photinia sonomensis	x	..	..
Picea sonomensis	..	..	x
Platanus paucidentata	..	x	x
Populus alexanderi	..	x	o
Populus pliotremuloides	..	x	..
Pseudotsuga sonomensis	x	..	x
Pteris calabazensis	..	..	x
Quercus bockéei	x	..	..
Quercus convexa	..	x	x
Quercus declinata	..	..	x
Quercus douglasoides	..	..	x
Quercus hannibali	..	x	x
Quercus lakevillensis	x	..	x
Rhamnus idahoensis	..	..	x
Rhododendron sp.	..	..	x
Salix boisiensis	x	..	..
Salix wildcatensis	x	..	x
Sequoia langsdorfii	x	x	x
Smilax sp.	x	..	..
Symphoricarpos salmonensis	..	..	x
Trapa americana	..	..	x
Tsuga sonomensis	..	..	x
Ulmus cf. tanneri	..	..	x
Umbellularia salicifolia	x	..	x
Vaccinium sonomensis	x	..	x
Total	18	12	37

o = species reported by Dorf, not encountered in present study.

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lived, the flora must be compared with the modern vegetation which resembles it most closely. Table 17, which lists the elements and components of the flora, provides a basis for such a discussion. Since the characteristic species of the Redwood Component, *Sequoia langsdorfii,* is common in the Petrified Forest and Neer's Hill florules and occurs also at Matanzas Creek, it is evident that major attention must be directed to this component. Three other components, the North-coast coniferous, Border-redwood, and Oak woodland, are represented by modern species which are found adjacent to the redwood forest. Taken as a group these four components include 39 modern representatives of the Sonoma flora.

Ten Sonoma species have their nearest modern equivalents in regions remote from the redwood forest. Two members of the Oak woodland Component, *Quercus convexa* and *Q. declinata,* find close living counterparts in *Q. engelmannii* and *Q. tomentella* of southern California. Their associates include 21 species having representatives in the Sonoma flora that are found with redwood. Two other members of the Oak woodland Component, *Ilex sonomensis* and *Mahonia prelanceolata,* now have equivalent species in the mountains of northern Mexico, and are interpreted as relicts of the Madro-Tertiary Flora that attained maximum development in west-central California in the Middle Pliocene. One of the common Sonoma species, *Persea coalingensis,* is a relict of the Caribbean Element which characterized central California in the early Tertiary. This species may also be assigned to the Oak woodland Component, for its modern equivalent, *P. podadenia,* lives in the oak country of northern Mexico with the two species noted above. Five other species are relicts of the Arcto-Tertiary Flora which survived in the coastal regions of central California into the later Pliocene. *Mahonia simplex, Quercus bockéei,* and *Trapa americana* are members of the East Asian Element, and *Castanea pliocenica* and *Ulmus* cf. *tanneri* belong to the East American.

Three areas where equivalents of the Redwood Component mingle with those of the North-coast coniferous, Border-redwood, and Oak woodland will now be considered in relation to the physical conditions of Sonoma time.

1. In the Santa Rosa region living equivalent members of the Redwood Component survive near those of the Oak woodland and Border-redwood (pl. 34, fig. 1). Twenty-three modern equivalent Sonoma species live within a radius of 12 miles of Santa Rosa. Most of these are distributed widely in the coastal parts of California and may range inland or southward for considerable distances.

2. In the Fort Bragg area on the Mendocino coast 80 miles northwest of Santa Rosa (pl. 35, fig. 2), modern representatives of the Redwood Component merge with those of the southern part of the North-coast coniferous. Twenty-six modern equivalent species occur here, and 5 of them, *Abies grandis, Rhamnus purshiana, Rhododendron californicum, Tsuga heterophylla,* and *Vaccinium parvifolium,* are characteristic modern correlatives of the mesic North-coast coniferous Component. Another species floristically related to this group, *Picea breweriana,*

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TABLE 17

ELEMENTS AND COMPONENTS OF THE SONOMA FLORA

Fossil species	*Equivalent living species*
West American Element	
Redwood Component	
Alnus rubroides	A. rubra Bongard
*Castanopsis sonomensis	C. chrysophylla A. DeCandolle
Ceanothus sp.	C. thyrsiflorus Eschscholtz
Lithocarpus klamathensis	L. densiflora (Hooker and Arnott) Rehder
Mahonia hollicki	M. aquifolium Pursh
Myrica sonomensis	M. californica Chamisso and Schlechtendal
Nymphaeites nevadensis	Nymphaea spp.
Pseudotsuga sonomensis	P. taxifolia (Lambert) Britton
Pteris calabazensis	P. aquilina Linnaeus
*Rhododendron sp.	R. californicum Hooker
Salix boisiensis	S. scouleriana Barratt
Sequoia langsdorfii	S. sempervirens Endlicher
*Umbellularia salicifolia	U. californica Nuttall
North-coast coniferous Component	
Abies sonomensis	A. grandis Lindley
*Picea sonomensis	P. breweriana Watson
Rhamnus idahoensis	R. purshiana DeCandolle
*Rhododendron sp.	R. californicum Hooker
Tsuga sonomensis	T. heterophylla Sargent
Vaccinium sonomensis	V. parvifolium Smith
Border-redwood Component	
Alnus merriami	A. rhombifolia Nuttall
Amorpha condoni	A. californica Nuttall
*Castanopsis sonomensis	C. chrysophylla A. DeCandolle
Cupressus sonomensis	C. macnabiana Murray
Fraxinus caudata	F. oregona Nuttall
Garrya masoni	G. elliptica Douglas
*Platanus paucidentata	P. racemosa Nuttall
Populus alexanderi	P. trichocarpa Torrey and Gray
Populus pliotremuloides	P. tremuloides Michaux
Quercus hannibali	Q. chrysolepis Liebmann
Salix wildcatensis	S. lasiolepis Bentham
Smilax sp.	S. californica Gray
Symphoricarpos salmonensis	S. albus Blake
*Umbellularia salicifolia	U. californica Nuttall
Southwest American Element	
Oak woodland Component	
Ceanothus precuneatus	C. cuneatus Nuttall
Ilex sonomensis	I. brandegeana Loesener
Mahonia prelanceolata	M. lanceolata Fedde
*Persea coalingensis	P. podadenia Blake
Photinia sonomensis	P. arbutifolia Lindley
*Platanus paucidentata	P. racemosa Nuttall
Quercus convexa	Q. engelmannii Greene
Quercus declinata	Q. tomentella Engelmann
Quercus douglasoides	Q. douglasii Hooker and Arnott
Quercus lakevillensis	Q. agrifolia Née

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TABLE 17—*Continued*

Fossil species	*Equivalent living species*
East American Element	
Castanea pliocenica	C. pumila Miller
Ulmus cf. tanneri	U. alata Michaux
East Asian Element	
Mahonia simplex	M. japonica DeCandolle
*Picea sonomensis	P. asperata Masters
Quercus bockéei	Fagaceae of several genera
Trapa americana	T. natans Linnaeus
Caribbean Element	
*Persea coalingensis	P. podadenia Blake

*Species occurring in more than one component.

occurs in the upper part of the Transition forest in the Klamath Mountain region. Along the coast it is replaced by *P. sitchensis* (Brongniart) Carrière, which ranges southward to Fort Bragg.

3. The redwood forest ranges southward into the Santa Lucia Mountains, and here it grows in proximity to living equivalents of the Oak woodland and Border-redwood Components. Twenty-six of the modern equivalent Sonoma species live in this region, which is notable for (*a*) marking the most southern occurrence of *Rhododendron californicum,* one of the mesic coastal species in the Sonoma flora, and (*b*) the common occurrence of *Platanus racemosa* along streams in the redwood forest.

The redwood forest has a limited distribution in the hills northeast of Santa Rosa, and occurs in the vicinity of the Petrified Forest, which is now at an elevation of about 900 feet. Redwood has largely been removed from the immediate vicinity of the fossil locality by logging, but is common in the deep canyons of Mark West Creek, within a mile of the locality, and on cooler slopes at higher elevations. Here its associates include the following:

Acer macrophyllum	Corylus californica
Alnus rhombifolia	Fraxinus oregona
Alnus rubra	Lithocarpus densiflora
Calycanthus occidentalis	Rhododendron occidentale
Ceanothus thyrsiflorus	Umbellularia californica

The removal of redwood from the fossil locality has resulted in the development of a border-redwood forest in the region, which is characterized by *Pseudotsuga taxifolia, Quercus garryana, Q. agrifolia,* and *Arbutus menziesii.* There is also a conspicuous chaparral association on the drier slopes, which is made up of such shrubs as *Adenostoma fasciculatum, Arctostaphylos stanfordianum, Ceanothus cuneatus, Cercocarpus betuloides, Pickeringia montana, Photinia arbutifolia,* and *Quercus dumosa.* The border-redwood forest occupying the upper parts of the hilly region east of Santa Rosa Valley extends along streams and cooler canyons into that valley, but is there subordinate to an oak savanna.

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The florule from the Petrified Forest suggests conditions cooler and moister than those found in that region today. This not only is indicated by a comparison of the fossil flora with modern vegetation in the vicinity of the fossil locality, but is particularly emphasized if the fossil flora is compared with vegetation now living at elevations comparable with those at which the Petrified Forest plant beds were laid down. The writer has not had opportunity to ascertain the exact amount of uplift at the Petrified Forest since Sonoma time. Judging from the degree of uplift in the adjacent region (Osmont, 1904, p. 78; Dickerson, 1922, p. 592; Morse and Bailey, 1935, p. 1454), there is reason to assume that the Forest is now situated at an elevation fully 500 feet above its original depositional level. It was thus laid down at an altitude which would fall well within the middle to lower part of the oak-savanna region which now characterizes Santa Rosa Valley. It probably was not more than a few hundred feet above the Neer's Hill and Matanzas Creek localities, which were essentially at sea level.

With respect to the florule at the Petrified Forest, it is significant that silicified redwood logs are sufficiently abundant to indicate that a forest of considerable extent lived in the area. In addition to *Sequoia,* the most abundant species here include *Pseudotsuga sonomensis* and *Quercus bockéei.* Added to this original group reported by Dorf are the new species *Abies sonomensis* and *Vaccinium sonomensis,* whose nearest modern relatives live on the humid coast of California 80 miles northwest. Thus it is evident that the Petrified Forest florule indicates conditions cooler and moister than are found in that region today. This conclusion is arrived at if the florule is compared with the border-redwood forest and chaparral communities dominating the locality today, or with the relict colonies of redwood living in the cool, shady canyons near the Petrified Forest, or, and more properly, with the oak savanna of the surrounding region at lower elevations.

The Neer's Hill and Matanzas Creek florules are located in Santa Rosa Valley. The valley is now largely under cultivation, but in certain areas relict stands of oak suggest that the valley formerly was characterized by *Quercus garryana, Q. lobata,* and *Q. agrifolia,* with *Q. douglasii* on the drier sites. The lower knolls throughout the valley contain such members of the border-redwood forest as *Arbutus menziesii* and *Quercus kelloggii,* and in certain areas *Pseudotsuga taxifolia* has a relict occurrence. Along the streams are *Acer macrophyllum, A. negundo* var. *californicum, Alnus rhombifolia, Populus fremontii, P. trichocarpa, Vitis californica,* and several species of *Salix,* as well as their common associates *Lonicera involucrata, Rhamnus californica, Rhus diversiloba, Rosa gymnocarpa,* and *Symphoricarpos albus.* The vegetation becomes more xeric in aspect north of Santa Rosa, owing to the higher Coast Range barrier at the west. In the region from Cloverdale, 20 miles north of Santa Rosa, northward for 30 miles to Hopland, there is a well developed *Pinus sabiniana–Quercus douglasii* association.

A comparison of the Neer's Hill and Matanzas Creek florules with modern vegetation in the Santa Rosa Valley indicates also that the fossil flora was more mesic than the present vegetation of these regions. The original collection from

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Neer's Hill includes *Sequoia,* which at once suggests a more moderate climate than prevails in that area today. An examination of more than 600 fossil leaves during the current study indicates that *Sequoia* was common in the region during Sonoma time. When this fact is considered together with the definitely coastal and mesic aspect suggested by the species of *Abies, Rhododendron, Rhamnus, Tsuga,* and *Vaccinium,* it seems certain that the Neer's Hill flora was considerably more mesic than the present oak savanna of that region. In this connection it should be noted that one of these plants, *Abies sonomensis,* is among the subdominants at this locality. It is significant also that the Neer's Hill florule contains such relicts of the Arcto-Tertiary Flora as *Castanea pliocenica, Trapa americana,* and *Ulmus* cf. *tanneri.* Likewise the Matanzas Creek assemblage has *Sequoia langsdorfii* and *Castanopsis sonomensis,* whose nearest descendants are indicators of a more humid climate than that characterizing the Santa Rosa Valley today.

The Sonoma flora has a closer relationship with the redwood forest near Fort Bragg, on the coast of central Mendocino County 80 miles northwest of Santa Rosa, than with the forest near Santa Rosa today. The vegetation and climate of the Fort Bragg area were discussed by Chaney and Mason in their study of the Santa Cruz Island flora of southern California (1930). The following statement includes some of their general observations, as well as additional data noted by the writer on a trip into the region. Emphasis will be directed toward an interpretation of the north-coast coniferous and redwood forests, rather than the closed-cone pine forest of this region, which shows relationship to the Pleistocene flora of Santa Cruz Island.

The Fort Bragg area comprises a relatively broad coastal plain which rises gradually to the coastal mountains known as the Mendocino Range. This coastal plain is traversed by numerous large streams, and except in their valleys the topography is gentle and rolling. The Mendocino Plain disappears some 10 to 12 miles south of Fort Bragg, where the hills come down to the ocean. The forest of this humid part of the California coast may be divided into three general types. The first is exemplified best by the dense redwood forest that covers the hills back of the immediate coast. This forest, which approaches the ocean only in the valleys that extend across the coastal plain, is dominated by *Sequoia sempervirens* and *Pseudotsuga taxifolia* and contains the following associates that also have equivalent species in the Sonoma flora:

Alnus rubra
Amorpha californica
Castanopsis chrysophylla
Ceanothus thyrsiflorus
Fraxinus oregona
Garrya elliptica
Lithocarpus densiflora
Mahonia aquifolium
Myrica californica
Populus trichocarpa
Pteris aquilina
Quercus agrifolia
Quercus chrysolepis
Rhamnus purshiana
Rhododendron californicum
Salix lasiolepis
Salix scouleriana
Smilax californica
Symphoricarpos albus
Umbellularia californica
Vaccinium parvifolium

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Near the coast, and particularly in the stream valleys facing the ocean, the dominant *Sequoia* and *Pseudotsuga* have as additional associates *Tsuga heterophylla* and *Abies grandis,* both of which have equivalent species in the Sonoma flora. These conifers form part of the second forest community which characterizes this region, namely the humid north-coast coniferous forest (the Coast forest of Clements, 1920), which attains its most southern limits near here. On the immediate coast *Abies* forms such dense stands that *Sequoia* and *Pseudotsuga* are largely subordinate or absent. Another coastal conifer, *Picea sitchensis,* also finds its most southern distribution in this area. It may be considered an ecological equivalent of *Picea sonomensis,* but the fossil seems more nearly related to *P. breweriana,* of the upper parts of the north-coast coniferous forest in northwestern California, 150 miles north. The restriction of members of the north-coast coniferous forest to the immediate coast region at Fort Bragg apparently is to be explained by the fact that fogs are more persistent here than in the redwood forest. The associates of these humid coastal conifers include most of the species listed above. Only the oaks and cottonwood have not been noted on the coastal slope at Fort Bragg. They occur a few miles inland, and approach the coast 30 miles south, where they are in proximity to *Abies grandis.*

The third forest association characterizing the Fort Bragg region is represented by the closed-cone pine forest. It is distributed along the sea cliffs, but attains greatest development on the flats separating the river valleys a short distance back of the coast. In this area, and particularly where the relatively level coastal plain breaks off into the river valleys, members of the closed-cone pine forest mingle with the other forest communities. Only two of the members of this forest, *Cupressus goveniana* and *Ceanothus thyrsiflorus,* have ecological counterparts in the Sonoma flora, and the latter is represented by a fragmentary specimen. The fact that none of the remaining species of the closed-cone pine forest have correlatives in the Sonoma flora suggests that that forest probably was not represented in the Santa Rosa region during Sonoma time. Notably absent from the Sonoma flora is *Arctostaphylos,* which forms a conspicuous under story in the *Pinus muricata–Cupressus goveniana* association. Since the three deposits representing the Sonoma flora come from both lowland and moderately upland habitats 15 miles apart, they would be expected to contain some of the equivalent members of the closed-cone pine forest if it had lived in the region. From a floristic standpoint, therefore, *Cupressus sonomensis* seems more nearly related to *C. macnabiana,* a characteristic member of the border-redwood forest from Napa and Lake counties northward into the Trinity-Shasta region and thence southward into the Sierra Nevada. The rarity of cypress in the flora, and the small size of the twigs, which suggests transport, indicate that it may have lived in sites remote from the immediate basin of deposition. *Cupressus sonomensis* is therefore believed to have occurred in the more exposed parts of the Santa Rosa basin together with members of the Border-redwood Component, rather than forming part of a closed-cone pine forest.

From this discussion it is evident that the Sonoma flora has much in common with the vegetation of the Fort Bragg region, an area where the redwood

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forest merges with the southern part of the north-coast coniferous. Two lines of evidence suggest that during Sonoma time this humid component lived in a region near its southern and interior limits of distribution. In the first place, members of the North-coast coniferous Component form a relatively small group in the Sonoma flora. Out of a total of 6 species that represent this forest, only the fir, *Abies sonomensis,* may be considered abundant; none of the remaining species is represented by more than 5 specimens. If this humid group had been living under conditions suited to its optimum development during Sonoma time, these plants would presumably have a greater representation in the flora. Secondly, the fact that members of the Border-redwood and Oak woodland Components are more numerous in the Sonoma flora than those of the North-coast coniferous also suggests that the latter was living in a region near its southern limit of distribution. The modern occurrence of these more arid components having equivalents in the Sonoma flora will now be considered, because they have an important bearing on an interpretation of the mesic group. Attention will be directed also to their northern limits of distribution near the coast, because in such areas certain members of the Border-redwood and Oak woodland Components approach those of the North-coast coniferous.

Twenty-six modern equivalent Sonoma species occur in the Santa Lucia Mountains, and 21 of these are represented also near Santa Rosa today. The redwood forest is limited largely to the seaward-facing canyons at low to moderate elevations in the Santa Lucia Mountains, where it is in proximity to border-redwood forest, chaparral, and oak savanna communities. The vegetation here is essentially like that already discussed for the Petrified Forest, but there are certain differences which must be noted. *Pseudotsuga taxifolia,* whose fossil equivalent, *P. sonomensis,* is a common Sonoma species, rarely occurs with *Sequoia* in the Santa Lucia Mountains. It increases in abundance in the Santa Cruz Mountains 50 miles north, and is common with redwood north of San Francisco Bay. The Santa Lucia region is notable for marking the most southern known occurrence of *Rhododendron californicum*, one of the typical members of the north-coast coniferous forest. Here it lives in a seaward-facing canyon in the northern part of the range near sea level. Its associates include *Sequoia* and the regular members of that community as found elsewhere in the Coast Ranges, as well as *Platanus racemosa,* which is a regular redwood associate in this region. *Rhododendron* is sparingly represented in the Santa Cruz Mountains to the north, and becomes abundant with redwood only in the coastal region from Mendocino County northward. Another feature of the Santa Lucia area is that *Quercus douglasii* reaches coastward along the Carmel River valley from the drier interior region, and occurs in proximity to redwood and within a few miles of *Rhododendron.* This oak also lives on drier slopes bordering the redwood forest in the Coast Ranges north of San Francisco Bay. The most northern and coastal localities observed by the writer for *Q. douglasii* are in the drainage of Austin Creek 40 miles southeast of Fort Bragg, where it occurs on serpentine exposures adjacent to a typical redwood forest, and near the headwaters of the south fork of the Gualala River another 10 miles north-

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west. It is significant that *Rhododendron* occurs also in this region, and that *Tsuga heterophylla* finds its present southern limit in this river valley some 6 or 7 miles from the coast.

Two of the modern equivalent Sonoma species, *Quercus engelmannii* and *Q. tomentella,* now live in southern California. *Quercus tomentella* is an insular endemic, but *Q. engelmannii* occurs on the mainland as well as on the Channel Islands. In this area they may live near *Alnus rhombifolia, Ceanothus cuneatus, Fraxinus oregona, Myrica californica, Photinia arbutifolia, Quercus chrysolepis, Symphoricarpos albus,* and *Umbellularia californica,* all of which have equivalent species in the Sonoma flora. The fossil equivalents of these oaks and semiarid species make up a minor part of the Sonoma flora as compared with the Redwood Component. But when they are considered together with *Platanus paucidentata* and *Quercus douglasoides,* it is evident that they had a more important place in the flora than the humid North-coast coniferous Component. Their comparative abundance in the Sonoma flora suggests that they lived on leeward slopes and in more exposed situations, not far from accumulating sediments.

The intermingling of members of the Border-redwood, Oak woodland, and North-coast coniferous Components in the Sonoma flora is of particular interest, for modern descendants of these plants are now living in distinct climatic and floristic provinces. It is believed that the presence of coastal conifers and their mesic associates in the flora necessarily implies maritime conditions during Sonoma time. An examination of the Pliocene floras of California shows a localization of climatic and floristic provinces which indicates that coastal conifers could have survived in the Santa Rosa area only if the flora was situated in a region where moderating coastal conditions were present during at least the drier parts of the year. Although such conifers as *Chamaecyparis, Picea, Sequoia,* and *Tsuga* are known to have had an interior distribution during Miocene time, in the later Tertiary they were largely limited coastward as rising mountain barriers blocked off the landward extension of maritime climate.

Coastal conditions extended into the Santa Rosa region during Sonoma time, but it is difficult to ascertain the exact position of the flora with respect to the ocean. Tuffaceous beds along the western border of Santa Rosa and Petaluma valleys have been interpreted as Sonoma volcanics interbedded in the marine Merced (Dickerson, 1922, pp. 544, 547–548). Judging from the areal distribution of these deposits, the Merced sea was situated largely to the south and west of the plant localities. It appears to have extended inland from the present site of Bodega Bay to the northeastern border of Petaluma Valley, and thence northward through Sebastopol to the present site of the Russian River, where it swings westward to the ocean. This position for the Merced sea 8 to 10 miles west and south of the Sonoma localities is indicated also by the character of the Sonoma sediments along the eastern side of Santa Rosa Valley. The presence of pebble beds and tuffaceous mud balls at the Matanzas Creek and Neer's Hill localities suggests deposition along a large coastal river, an inference which agrees with Osmont's original observations in the area directly north of these localities

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(1904, p. 74). Furthermore, the fact that marine invertebrates have not been found on the eastern side of the valley suggests also that the strand lay to the west. The general picture afforded by these data is of a region of low to moderate relief (Dickerson, 1922, p. 547) traversed by a large river valley. Within a distance of 5 to 10 miles the river merged into estuaries and then into the strand region, where marine invertebrates were preserved in the tuffaceous beds.

This position for the Sonoma flora suggests that the mesic North-coast coniferous Component may have extended from the coastal area up a broad valley into the Santa Rosa region. Corroborative evidence for this interpretation is provided by the Border-redwood and Oak woodland Components, which lived on leeward and exposed slopes surrounding the Sonoma sites of deposition. Their relatively large numerical representation in the flora, as compared with the North-coast coniferous Component, suggests that the plant localities were situated near the inland limits of the latter group. In such an area the North-coast coniferous Component would be expected to have a poor representation in the flora, and, as noted elsewhere, all its species except *Abies sonomensis* are rare. Furthermore, they would presumably be living under conditions comparable with those which are found today near their southern limits of distribution. Heavy fogs now control the distribution of the north-coast coniferous forest in the southern part of its range, as well as at the interior. Only a short distance south of Fort Bragg, or inland, where fogs are less persistent than along the coast, summer temperatures are slightly higher and evaporation is greater. In these areas the characteristic north-coast coniferous forest species are absent and are replaced rapidly by members of the border-redwood community.

Thus it is believed that the North-coast coniferous Component of the Sonoma flora was limited largely to the cooler north slopes of a river valley, in much the same manner as they are distributed today in the Fort Bragg region. Such an interpretation seems to account for the otherwise peculiar intermingling of humid coastal conifers and southern woodland plants. It is difficult to explain the mixture of *Platanus paucidentata, Quercus convexa,* and *Q. declinata* with *Abies sonomensis, Rhododendron* sp., and *Tsuga sonomensis* on any other basis.[2] On a later page it will be pointed out that the oaks and sycamore are members of an element that characterized this region in pre-Sonoma time. They represent the last survivors of the Madro-Tertiary Flora, which was replaced in this area by more humid vegetation in the Upper Pliocene. During Sonoma time they formed a community on leeward slopes and exposed sites in the Santa Rosa region together with certain members of the border-redwood forest. In such localities the high summer fogs would be dissipated more rapidly than at the immediate sites of deposition, where low and heavy fogs were sufficient to account for the presence of the coastal conifer component in the redwood forest.

[2] In reply to the suggestion that the southern group may have been transported from distant interior areas into the Santa Rosa basin, it may be pointed out that the leaves, which are preserved in a fine-grained tuffaceous silt, are mostly complete and show no evidence of transport for great distances.

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The present climate of the Fort Bragg region provides a general index to conditions about the immediate site of Sonoma deposition, because this is the area where the north-coast coniferous forest reaches its southern limits of distribution. Modifications necessary to account for the Border-redwood and Oak woodland Components, as well as the East American, East Asian, and Caribbean Elements, will be indicated in the following discussion. Climatic data at Fort Bragg, at an elevation 70 feet above sea level, show an annual average rainfall of 37 inches, falling chiefly during the period from October to May. Rainfall is higher in the hilly region back of the town, and also increases southward along the coast where the hills approach the ocean. It is believed that the north-coast coniferous and redwood forests in this region live under an annual rainfall of 40 inches yearly, probably exceeding 45 inches near the crest of the coastal slope. This region is subject to almost daily fogs, which are particularly heavy during the summer months. As a result of condensation of fog on the trees there is an appreciable fog drip during the summer, which often is sufficient to make the ground wet and muddy beneath the trees. Owing to its coastal position and these heavy fogs, the temperature of the Fort Bragg area is characterized by a low daily and a low annual range. Temperature data are not available for Fort Bragg, but because similar conditions extend along the coast for many miles north and south, it is believed that an evaluation of temperature data for stations at Eureka and Point Reyes will provide an index to Fort Bragg conditions.

From Eureka, 95 miles north, to Point Reyes, 110 miles south of Fort Bragg, there is a difference of only 1° F. in average annual temperature—from 51.6° F. at Eureka to 52.5° F. at Point Reyes. The three hottest summer months at both of these stations have an average maximum of 60° F.; the average minimum temperature for the three coldest months ranges from 53° F. at Eureka to 54° F. at Point Reyes. Conditions at Fort Bragg are considered to be closely similar. The extreme temperatures recorded at these coastal stations north and south of Fort Bragg are as follows: The highest summer temperature at Eureka is 85° F., and at Point Reyes it is 98° F.; Fort Bragg presumably has summer extremes in the neighborhood of 90° F. The lowest temperature recorded at Eureka is 20° F., and at Point Reyes 30° F.; a low of 25° F. for Fort Bragg may be regarded as approximate.

A comparison of the present climate at Santa Rosa with that indicated above for Fort Bragg provides an index to the degree of climatic change in the Santa Rosa region since Sonoma time. The Neer's Hill and Matanzas Creek localities are 2 miles north and 3 miles southeast of Santa Rosa, respectively (Dorf, 1930, pp. 12–13). Because the original level of deposition of the Petrified Forest is believed to have been not more than a few hundred feet above these localities, climatic data for Santa Rosa also give a general indication of conditions for the Petrified Forest. Table 18 shows that the climate has changed appreciably in the Santa Rosa region since Sonoma time. The difference in total rainfall between Santa Rosa and Fort Bragg suggests that annual rainfall has been lowered fully 10 inches since the Sonoma epoch. In addition, there has been a

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TABLE 18

COMPARISON OF CLIMATIC DATA AT FORT BRAGG AND SANTA ROSA

	AV. ANN. RAINFALL (IN.)	AV. ANN. TEMPERATURE (°F.)	AV. 3 HOTTEST SUMMER MONTHS (°F.)	AV. 3 COLDEST WINTER MONTHS (°F.)	EXTREMES	
					High (°F.)	Low (°F.)
Santa Rosa.....	29	57	81	36	112	15
Fort Bragg.....	40	52	60	53	90	25

marked rise in average annual temperature, summers are hotter, and winters are colder than those of Sonoma time.

The figure of 40 inches of rainfall for the Sonoma epoch is considered to represent conditions only at the immediate site of deposition, where the North-coast coniferous and Redwood forests were contributing their leaves and seeds to accumulating sediments. The Border-redwood and Oak woodland Components, which form important groups in the flora, lived on leeward and exposed slopes in the Santa Rosa region. Judging from rainfall data for areas where these communities approach the more mesic parts of the redwood forest, it is believed that they lived under an annual rainfall of about 35 inches during Sonoma time. In view of the fact that fogs were less persistent in this region than at the immediate sites of deposition, the effective rainfall in these areas may have been lower. With respect to the Sonoma oaks whose modern equivalents now occur in southern California, it may be noted that they also range into areas where rainfall is in the neighborhood of 30 to 35 inches yearly.

Five Sonoma species, *Castanea pliocenica, Mahonia simplex, Quercus bockéei, Trapa americana,* and *Ulmus* cf. *tanneri,* have their nearest equivalents in the eastern United States and eastern Asia, regions where rainfall is distributed rather evenly throughout the year. Three members of the Southwest American and Caribbean Elements, *Ilex sonomensis, Mahonia prelanceolata,* and *Persea coalingensis,* are represented by species now living in Mexico, a region where summer rains are characteristic. Since 5 of these genera, *Castanea, Trapa, Ilex, Persea,* and *Ulmus,* and all the modern equivalent species now survive in regions with summer rains, it is concluded that summer precipitation occurred in Sonoma time. The low numerical representation of these plants in the Sonoma, however, as compared with their dominance in the Miocene and early Pliocene floras of the coastal region, suggests that total summer precipitation during the Sonoma stage was lower than it had been earlier in the epoch. It is difficult to estimate the amount of rainfall that may have occurred during this season, but it must have been much lower than the total winter precipitation.

The general physical conditions which appear to have characterized the Santa Rosa region during Sonoma time may be summarized as follows:

1. The Sonoma flora was preserved in fine-grained volcanic sediments which accumulated in a large coastal river within a few miles of the ocean (Neer's Hill and Matanzas Creek), and also includes plant remains preserved in a

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coarse tuff which was deposited subaerially within a few hundred feet of sea level (Petrified Forest). The low coastal hills now lying to the west were not in existence during Sonoma time.

2. A North-coast coniferous Component of *Abies, Picea,* and *Tsuga,* with their characteristic associates *Rhamnus, Rhododendron,* and *Vaccinium,* extended up a broad coastal river valley and into the Santa Rosa region, where they mingled with a typical Redwood Component. In addition to *Sequoia,* this forest contained species of *Alnus, Castanopsis, Ceanothus, Lithocarpus, Mahonia, Myrica, Salix,* and *Umbellularia,* all of which have survived down to the present in modified form in coastal California and make up an integral part of the redwood forest. Certain genera which were associated commonly with redwood in the Miocene at the north, such as *Castanea, Trapa,* and *Ulmus,* have a relict occurrence in the Sonoma flora.

3. The leeward slopes and drier sites about the region were inhabited by members of the Border-redwood Component, and here also was the Oak woodland Component, which had dominated this area somewhat earlier in the Pliocene.

4. The climate during Sonoma time was characterized by an annual rainfall of 35 to 40 inches, and there is evidence also of summer precipitation during this stage. Owing to the heavy coastal fogs which extended up the valley into the Santa Rosa area, temperatures in the north-coast coniferous and associated redwood forests had a low daily and a low annual range. Members of the Border-redwood and Oak woodland Components lived in sites where fogs were less persistent, and where rainfall was somewhat lower and evaporation greater.

Age of the Flora

In the introduction to this chapter, it was pointed out that a general age assignment may be given to a Pliocene flora in west-central California on the basis of its climatic implications. A more exact position within any one of the three subdivisions of the Pliocene may be estimated from a detailed floristic analysis (Chaney, 1938*a*; Axelrod, 1938; 1940*b*, pp. 484–486). Both of these methods will be employed in the following discussion.

As now understood, the changing character of vegetation and climate during the Pliocene in west-central California was essentially as shown in table 19. If the Sonoma flora is evaluated with respect to this table, its age is necessarily Upper Pliocene, because Sonoma climate was characterized by heavier rainfall and more moderate temperatures than occur in the Santa Rosa region today. The objection might be raised that the flora is equally referable to the Lower Pliocene, for conditions during that stage were also more moderate than those today. Lower Pliocene floras in west-central California, however, are dominated by the East American and East Asian Elements, which are rare at Sonoma. The relict occurrence of members of these elements in the flora (*Castanea pliocenica, Mahonia simplex, Quercus bockéei, Trapa americana,* and *Ulmus* cf. *tanneri*) suggests that the Sonoma may belong to the early, rather than to the later, part of the Upper Pliocene. This is the first record of these plants so late in the Plio-

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cene; their complete stratigraphic ranges are not known, but it is believed that they did not survive into late Upper Pliocene time in this region. This conclusion is suggested by the fact that collections of the Santa Clara flora by Hannibal, Chaney, and Dorf (Dorf, 1930) in the region 80 miles south have failed to reveal any members of these elements. On this basis the Santa Clara is considered to be of post-Sonoma age; it probably represents the later part of Upper Pliocene time and may possibly be of basal Pleistocene age.

The assumption of an early Upper Pliocene age for the Sonoma is strengthened further by the occurrence of such members of the Southwest American and Caribbean Elements in the flora as *Ilex sonomensis, Persea coalingensis,* and

TABLE 19

SUCCESSION OF VEGETATION AND CLIMATE IN WEST-CENTRAL CALIFORNIA DURING THE PLIOCENE

Division of Pliocene	*Vegetation*	*Climate*
Upper	Flora more mesic than modern vegetation of the region. Reduction in numbers of the Southwest American Element. Arcto-Tertiary species present only in the early part of the stage.	Cooler and moister than today. Summer rains early in the stage.
Middle	Dominated by the Southwest American Element. Arcto-Tertiary species not common; limited to cooler upland habitats with the border-redwood community.	Drier and warmer than today. Biseasonal rainfall.
Lower	Characterized by members of the Arcto-Tertiary Flora, which are partly replaced later in the stage by the Southwest American Element.	Humid and more moderate than today. Gradual change from even to biseasonal rainfall.

Mahonia prelanceolata, now represented by species in Mexico. Three other species belonging to the Southwest American Element, *Platanus paucidentata, Quercus convexa,* and *Q. declinata,* have equivalents in areas south of Santa Rosa; the oaks occur in southern California. The Southwest American Element became abundant in west-central California near the end of Lower Pliocene time, and attained optimum development during the Middle Pliocene. Its moderate representation in the Sonoma suggests that the flora probably is of early Upper Pliocene age. It is critical that members of this element with surviving relatives to the south have not been encountered in the Santa Clara flora. Their absence here gives greater credibility to the post-Sonoma age of the Santa Clara, as well as to the early Upper Pliocene age of the Sonoma.

Corroborative evidence with respect to this age assignment for the Sonoma flora is afforded by a consideration of fossil plants and vertebrates from the near-by region. It has already been pointed out that the Sonoma is underlain un-

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conformably by the Petaluma formation in the region southeast of Santa Rosa (Morse and Bailey, 1935). These beds contain both plant and vertebrate material which has a direct bearing on the age of the Sonoma. The Petaluma formation has been divided by Morse and Bailey into a lower and an upper member. The Lower Petaluma is from 500 to 600 feet thick and consists largely of thin-bedded clay shales, yellow-brown sandstones, and limestones. The occurrence of fish remains, ostracods, and shell fragments, together with the character of sorting and lamination of the sediments, suggests an estuarine origin for this member. This lower part of the formation grades downward into the Tolay volcanics, which are about 4000 feet thick. The Upper Petaluma consists chiefly of poorly stratified clays, sands, and gravels, totaling some 3500 feet in thickness.

The occurrence of plant remains in the upper part of the Lower Petaluma was reported by Morse and Bailey (1935, p. 1444), and the writer has made a small collection at this locality. The flora occurs in the middle of the first large road cut along the county road, directly east of the Lakeville School, Petaluma Quadrangle. Leaf impressions are preserved in a yellow-brown, sandy clay stratum a foot thick. This lies above a coarse sandstone member 15 feet thick, and 30 feet below a 12-foot pebble bed which seems to mark the basal part of the Upper Petaluma. The lower beds dip 80° to 83° northwest, but several hundred feet eastward the attitude of the Upper Petaluma decreases to 30° and 40° northwest. The plants that have been collected from this horizon are listed below, and those that are particularly abundant are marked by an asterisk (*):

Arbutus matthesii Chaney
Ceanothus precuneatus Axelrod
Fraxinus caudata Dorf
*Platanus paucidentata Dorf
*Populus alexanderi Dorf
Quercus hannibali Dorf
*Quercus moragensis Axelrod
Quercus orindensis Dorf
*Quercus wislizenoides Axelrod
Salix hesperia (Knowlton) Condit
*Salix wildcatensis Axelrod
Ulmus moragensis Axelrod
Umbellularia salicifolia (Lesquereux) Axelrod

In connection with the interpretation of the Sonoma flora, it is to be noted that the Petaluma is characterized by an oak savanna-woodland and its common flood-plain associates. Members of the Border-redwood Component form a distinctly minor group. The Lower Petaluma flora is more xeric than the present vegetation of the adjacent Coast Ranges, and is more nearly comparable with the modern forests found in the inner parts of the Santa Cruz and Santa Lucia mountains to the south. Since the Petaluma flora is drier than the Sonoma flora, and is dominated by members of the Southwest American Element, it is necessarily older. This age assignment agrees with its stratigraphic position, unconformably below the Sonoma. On the basis of the relative development of its northern and southern elements, the Lower Petaluma flora is considered to be not older than Middle Pliocene.

In connection with the Petaluma flora, it must be pointed out that the Merced

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flora reported by Dorf, which occurs at a locality 1½ miles south of the Lower Petaluma flora, probably comes from the Petaluma formation. Morse and Bailey (1935), as well as Dorf (1930, p. 16), have noted a thick tuff bed interbedded in the formation directly south of the fossil locality. Although this member has been interpreted as representing part of the Sonoma group interbedded in the marine Merced, Morse and Bailey have assigned it to the Upper Petaluma. They point out that it crops out also in the vicinity of Adobe Fort 5 miles northwest, where it is stratigraphically near the *Neohipparion gidleyi* horizon, and unconformably below the Sonoma. Another feature suggesting that these beds are properly referable to the Petaluma is the occurrence of pebble beds containing Monterey chert and Franciscan-derived material. Dickerson originally defined the Petaluma in this manner, but he has mapped the area under consideration as Merced (1922, p. 548, pl. 17). These data suggest that the following species reported from the Lakeville locality are referable to the Petaluma formation:[8]

Platanus paucidentata Dorf
Quercus lakevillensis Dorf
Umbellularia salicifolia (Lesquereux) Axelrod
Populus prefremontii Dorf
Castanopsis chrysophylloides Lesquereux (Dorf not Lesquereux) (possibly Quercus hannibali Dorf)
Salix coalingensis Dorf (possibly Salix wildcatensis Axelrod)
Alnus merriami Dorf

The list above represents in descending order the relative abundance of the species at this horizon (Dorf, 1930, p. 17). The flora is essentially identical with the larger collections made in the lower part of the formation.

One other coastal Pliocene flora that may be compared with the Sonoma is the Wildcat, near Garberville (Dorf, 1930, pp. 46–48), 130 miles northwest. On the basis of additional collections, the following species are now considered to represent this flora:

Alnus cf. rubroides Axelrod
Alnus merriami Dorf
Fraxinus caudata Dorf
Persea pseudo-carolinensis Lesquereux
Platanus paucidentata Dorf
Populus eotremuloides Knowlton
Pseudotsuga sonomensis Dorf*
Salix wildcatensis Axelrod
Sequoia langsdorfii (Brongniart) Heer*
Ulmus sp.
Umbellularia salicifolia (Lesquereux) Axelrod

*Represented only by fossil wood from a locality 3 miles south of the leaf horizons.

Eight of these 11 species occur in the Sonoma, and 2 of the other genera, *Populus* and *Persea,* have similar species in the Sonoma. The Wildcat cottonwood has been referred to *Populus eotremuloides* rather than to *P. alexanderi* Dorf on the basis of its greater dimensions and comparatively large teeth. The avocado at Wildcat seems to represent *Persea pseudo-carolinensis* rather than

[8] Recent systematic revisions have been incorporated in this list.

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the more slender *P. coalingensis* of the Sonoma; further collections, however, may show that they represent the same species. The Wildcat elm, as represented by an incomplete small leaf, is a member of the East Asian or East American Element. Members of these elements in the Sonoma include also species of *Castanea, Mahonia, Quercus,* and *Trapa.*

The Wildcat flora was laid down on a broad flood plain on the edge of a marine embayment that extended into the Garberville region from the northwest (Dorf, 1930, pp. 46–47). In view of this depositional site, it is not surprising to find that the flora is dominated by flood-plain species of alder, ash, cottonwood, avocado, sycamore, and willow, and that *Sequoia* and *Pseudotsuga* are represented only by logs. The broad flood plains of many rivers adjacent to the ocean today, for example the Carmel, Sur, and Russian, are completely dominated by flood-plain species, with forests restricted to the bordering hills. The poor representation of *Sequoia* and its regular forest associates, and the extraordinary development of the flood-plain assemblage, seem explainable on this basis.

From the material at hand, it is difficult to estimate closely the total rainfall of Wildcat time. In the writer's opinion there is no direct evidence for a drier climate at Garberville during Wildcat time than is found there at present. The poor representation of redwood and the dominance of flood-plain species seem more probably due to a depositional site near the mouth of a large river valley away from forests. Further collections at the Wildcat locality may reveal certain forest members other than *Sequoia* and *Pseudotsuga.* On the basis of our more recent knowledge of the Pliocene floras of California, they may be expected to include representatives of the Redwood and North-coast coniferous Components, rather than those of the Border-redwood or Oak woodland.

Although it is not now possible to determine the total annual rainfall of Wildcat time, certain species in the flora provide evidence with respect to other climatic features. The sycamore and avocado suggest warmer conditions than those in northwestern California today. Elm and avocado provide a basis for suggesting that there were summer rains during this stage.

The Wildcat flora is Upper Pliocene in age. This is indicated by its position directly above the Upper Wildcat invertebrate fauna, which is now considered to be of Upper Pliocene age (Woodring *et al.,* 1940, p. 109 and table facing p. 112). From a floral standpoint it is also evident that the Wildcat belongs to the Upper Pliocene. The poor representation of the East Asian and East American Elements strongly suggests such an age assignment, as set forth elsewhere in this report.

The Wildcat and Sonoma floras are closely related, as was originally pointed out by Dorf. The differences between them were probably due to differences in habitat. The Sonoma was laid down in a region of moderate relief where members of the Redwood, North-coast coniferous, Border-redwood, and Oak woodland Components adjusted themselves with respect to exposure. The position of the Wildcat on a flood plain near the sea apparently accounts for the absence of leaves of forest trees in its sediments. Greater similarities between

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these floras may be expected when larger collections are available at Wildcat.

Summarizing the evidence for the Upper Pliocene age of the Sonoma flora, the following points may be noted:

1. The flora indicates climatic conditions characteristic of the early part of Upper Pliocene time in west-central California.

2. The Sonoma is underlain unconformably by the Petaluma formation, which contains a flora in its lower part that is not older than Middle Pliocene.

3. The uppermost part of the Petaluma contains the *Neohipparion gidleyi* horizon, whose age has been considered not older than late Middle Pliocene.

4. Marine invertebrates of probable Upper Pliocene age occur in Sonoma tuffs which are intercalated in the Merced formation on the western side of Santa Rosa and Petaluma valleys.

Since this chapter was completed, a new Sonoma florule of about 25 species has been collected in the tuffs near Napa, 35 miles southeast of Santa Rosa. It is dominated by the Border-redwood Component of the West American Element and also has an important Oak woodland Component. The Redwood Component is highly restricted, and there is also a small representation of the Sierra-Cascade Component. The absence of members of the North-coast coniferous Component, as well as the East Asian and East American Elements, shows that they survived only in close proximity to moderating coastal conditions in west-central California in Sonoma time. Such differences are readily explainable on the basis of the more inland position of the Napa florule, and are to be expected in the Pliocene. The Napa florule is sufficiently more mesic than both the Middle Pliocene Petaluma flora to the west, and modern vegetation at the fossil locality today, to suggest its early Upper Pliocene age. If it is Middle Pliocene, it can belong only to the latest part of that stage.

Summary

The Sonoma flora of 44 species finds closest relationship to three components of the Arcto-Tertiary Flora which have survived in modified form in coast-central California: the redwood, north-coast coniferous, and border-redwood forests. In addition there are relicts of the Arcto-Tertiary Flora whose nearest relatives now occur in northeastern Asia and eastern North America, and a few members of the Madro-Tertiary Flora which migrated northward from Mexico into the western United States during mid-Tertiary time.

Sonoma climate differed from that of today in having higher annual rainfall, some summer precipitation, heavier summer fogs, and lower ranges of yearly and seasonal temperatures.

On the basis of its position in the climatic and floristic sequence in west-central California, the Sonoma flora is considered to be Upper Pliocene in age. This interpretation agrees with plant and vertebrate evidence from the underlying Petaluma formation, and is in harmony with the probable age indicated by marine invertebrates collected from tuffaceous beds of Sonoma origin intercalated in the Merced formation at the west.

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SYSTEMATIC DESCRIPTIONS

Phylum PTERIDOPHYTA

Family POLYPODIACEAE

Pteris calabazensis Dorf

Pteris calabazensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 67–68, pl. 5, figs. 1, 2, 1930.

A terminal part of a pinna, with several lateral pinnules showing terminal sori, is clearly representative of the genus *Pteris*. Although it is referred to the Pliocene species, it may not be distinct from the Miocene *Pteris silvicola* Hall (Chaney, 1927) or *P. idahoensis* (Knowlton) Brown (Brown, 1940). All of them resemble the modern *Pteris aquilina* Linnaeus, a cosmopolitan species.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2623.

Phylum SPERMATOPHYTA

Class GYMNOSPERMAE

Family PINACEAE

Abies sonomensis new species

(Plate 36, figures 4, 7)

Description. Needles both long and short, 1.1 to over 2.5 cm. long, but mostly of the smaller size; 2 mm. wide in the larger needles to 1.5 mm. in the smaller; tip blunt and with a notch at the apex; petiole short. Body of seed 4.0 to 4.5 mm. long, complete wing preserved only in the smaller seeds, measuring 8.0 mm. long and 6.0 mm. wide at the top; larger wings more than 1.0 cm. long (estimated).

Discussion. On the basis of the notched needles, this fir material is considered to represent the Pliocene equivalent of the modern *Abies grandis* Lindley. Although the seeds are not sufficiently well preserved to be distinguished from those produced by certain other living species of fir, they do not reveal any features suggesting they may not be related to *A. grandis*. The lowland white fir is a common California species ranging from the coast near Fort Bragg, 40 miles northwest of Santa Rosa, northward into Washington and thence eastward to Idaho. In areas of its southern distribution it is confined to canyons along the immediate coast, where it receives almost daily fogs.

Occurrence. Neer's Hill, loc. 154; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, nos. 2624, 2624*a* (counterpart) (loc. 154); paratype, no. 2625 (loc. 150); nos. 2626, 2627, 2628, 2629, 2630 (loc. 154).

Picea sonomensis new species

(Plate 36, figure 2)

Pinus sp. Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 722, pl. 99, fig. 3, 1898.
Pinus sp. Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 168, pl. 45, fig. 15, 1937.
Picea sp. Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 168, pl. 45, figs. 18, 19, 1937.

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Picea lahontense MacGinitie. H. V. Smith, Papers Mich. Acad. Sci., Arts and Letters, vol. 23, p. 224, pl. 1, fig. 9, 1938.

Pseudotsuga masoni MacGinitie. Oliver, Carnegie Inst. Wash. Pub. 455, I, p. 14, 1934.

All this material is alike in having a wing of the same shape and a seed with a snubbed nose on the upper side.

Description. Complete seed long oval, the wing 2 to 3 times as long as the seed; total length 1.0 to 1.5 cm., width 3 to 5 mm. at the greatest width of the wing, which is in the outer part; end of wing rounded to subacute; seed oval, with a snubbed nose.

Discussion. Among modern American species of this genus, *Picea sonomensis* is most closely similar to the seeds produced by *Picea breweriana* Watson, which is now endemic to the Klamath Mountain region of northwestern California and adjacent Oregon. The weeping spruce has a vertical range of from 4500 to over 7000 feet in areas of its present distribution, and at lower levels is commonly associated with such members of the Transition forest as *Abies concolor, Libocedrus decurrens, Pinus lambertiana,* and *Pseudotsuga taxifolia.*

There are several Asiatic species which produce seeds similar to those of *P. breweriana* and *P. sonomensis.* Among these may be mentioned *P. asperata* Masters, *P. likiangensis* Pritzel, *P. meyeri* Rehder and Wilson, *P. morinda* Link, and *P. wilsoni* Masters.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2631.

Pseudotsuga sonomensis Dorf

(Plate 36, figure 3)

Pseudotsuga sonomensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 72–73, pl. 6, figs. 2–4, 1930.

In the writer's opinion the figured Sonoma specimen represents an unquestionable record of a seed of *Pseudotsuga* in the Tertiary of western North America. The type material of *P. masoni* MacGinitie (1933) apparently represents another genus. The seeds of *P. masoni* differ from those of the modern *P. taxifolia* (Lambert) Britton in that the fossil seeds are rounded, whereas those of the modern species are sharply angled at the uppermost point of attachment with the wing. Another important point of difference is that the tip of the wing is rounded in *P. masoni,* whereas in the living Douglas fir it is regularly acute. It would appear that the type material of *P. masoni* from Trout Creek may represent *Pinus* rather than *Pseudotsuga.*

As noted above under *Picea sonomensis,* the records of *Pseudotsuga masoni* from the Idaho and Austin-Tipton floras apparently represent *Picea* rather than *Pseudotsuga.*

A bract and seed recently figured by H. V. Smith from the Thorn Creek flora as *Pseudotsuga masoni* (1941) appear to represent *Pseudotsuga,* but it is necessary to examine those specimens before making a definite statement about their taxonomic position.

Occurrence. Neer's Hill, loc. 154; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 310, 311 (loc. 150); plesiotypes, nos. 313 (loc. 150), 2632 (loc. 154); no. 2633 (loc. 150).

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Tsuga sonomensis new species

(Plate 36, figures 5, 6)

Description. Seeds of variable size; largest 9.0 mm. long and 3.5 mm. wide at widest part of the wing; smallest 5.5 mm. long and 2.0 mm. wide; body of seed from ¼ to ⅓ the size of the wing, roughly triangular in outline; wing extended under seed, widest at or near middle, tapering to an asymmetrically acute tip.

Discussion. These coniferous seeds closely resemble those produced by the modern *Tsuga heterophylla* Sargent of the western United States. In California the coastal hemlock ranges southward along the coast into Mendocino County, and is abundant as far as the Fort Bragg region. Its most southern known station is on the south fork of Gualala River several miles east of Plantation, an area 50 miles northwest of Santa Rosa. Sudworth (1908, p. 94) reports it from Marin County, but it is not known there today; it may have been destroyed by fire and logging.

The only other probable Tertiary record of the genus in the western United States is the cone material figured by Brown as *Picea,* which he indicates may be *Tsuga* (Brown, 1937*a,* p. 167, pl. 45, figs. 29, 30). Examination of this material by the writer suggests a closer relationship to *Tsuga* than to *Picea.*

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, nos. 2634, 2634*a* (counterpart); paratype, nos. 2635, 2635*a* (counterpart).

Family TAXODIACEAE

Sequoia langsdorfii (Brongniart) Heer

Sequoia langsdorfii (Brongniart) Heer, Flora tertiaria Helvetiae, vol. 1, p. 54, pl. 20, fig. 2; pl. 21, fig. 4, 1855.

During the current studies leafy twigs of *Sequoia* have been found to be rather common at the Neer's Hill locality. Judging from Chaney's extensive studies of the modern redwood forest, which indicate that leafy twigs of the coast redwood are not transported for any considerable distance by streams (1927, p. 102), it would appear that *Sequoia* lived near the Neer's Hill site of deposition.

Occurrence. Neer's Hill, loc. 154; Matanzas Creek, loc. 152; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 317 (loc. 154); nos. 2636, 2637 (loc. 154), 2638 (loc. 152), 2639 (loc. 150).

Family CUPRESSACEAE

Cupressus sonomensis new species

(Plate 36, figure 1)

Description. Terminal part of a leafy branchlet 8 mm. long and 1 mm. wide; the scale leaves opposite and with blunt tips; each scale leaf slightly less than 1 mm. long.

Discussion. This material undoubtedly represents *Cupressus,* but from a taxonomic standpoint it is not possible to relate it definitely to any one living species of the genus in California. From an ecological standpoint, however, it seems probable that *C. macnabiana* Murray may represent its nearest modern correlative (page 178).

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This species is distributed from the Coast Ranges in Napa and Sonoma counties northward into Shasta and Siskiyou counties, and thence southward into the central Sierra Nevada. It is found commonly with the border-redwood forest and its related communities.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, nos. 2640, 2640*a* (counterpart); no. 2641.

Class ANGIOSPERMAE
Subclass MONOCOTYLEDONES
Family LILIACEAE

Smilax sp. Dorf

Smilax sp. Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 74–75, pl. 6, fig. 7, 1930.

Only the single specimen recorded and figured by Dorf has been encountered in the Sonoma flora. Owing to the fact that it is curled in the ashy matrix, it is actually larger than the published figure would indicate. It does not appear to differ from *Smilax diforma* Condit of the Neroly flora (1938), and further collections may show them to be identical.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 323.

Subclass DICOTYLEDONES
Family SALICACEAE

Populus alexanderi Dorf

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, figs. 10, 11 (not fig. 9, which is *P. prefremontii* Dorf); pl. 7, figs. 2, 3 (not fig. 1, which is *P. prefremontii*), 1930.

Condit, Carnegie Inst. Wash. Pub. 553, p. 40, 1944 (see synonymy).

A nearly perfect specimen representing this species has been encountered in the collections from the Matanzas Creek locality. *Populus trichocarpa* Torrey and Gray, which closely resembles the fossil species, now lives near the fossil locality.

Occurrence. Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotype, no. 324; nos. 2642, 2643.

Populus pliotremuloides Axelrod

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 169–170, pl. 4, figs. 1–3, 1938.

Leaves of this species have been found to be common in the collections from the Matanzas Creek locality. *Populus prefremontii* Dorf has been reported as abundant at this locality, but this cottonwood has not been encountered in the collections. Because the smaller leaves of *P. prefremontii* may bear a superficial resemblance to those of *P. pliotremuloides,* the writer is of the opinion that the so-called leaves of *P. prefremontii* at this locality are in reality those of the Pliocene aspen.

Occurrence. Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2644, 2645.

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Salix boisiensis H. V. Smith

(Plate 36, figures 8–10)

Salix boisiensis H. V. Smith, Amer. Midland Naturalist, vol. 25, p. 498, pl. 2, fig. 3; pl. 4, fig. 8, 1941.

Several willow leaves from the Petrified Forest locality are closely similar to those of the modern *Salix scouleriana* Barratt (*S. nuttallii* Sargent) of the western United States. In the Fort Bragg region it is a particularly abundant species along streams in the redwood and humid north-coast coniferous communities.

Only one other fossil willow has been noted by the writer which resembles *S. boisiensis* in any important respect. This is *S. libbeyi* Lesquereux from Florissant, and further collections there may show that the species are not distinct.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2646, 2647, 2648.

Salix wildcatensis Axelrod

Salix wildcatensis Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

The upper half of an entire-margined willow leaf is represented at each of two localities. On the basis of their resemblance to the modern *Salix lasiolepis* Bentham of California, the specimens are referred to this fossil species.

Occurrence. Petrified Forest, loc. 150; Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2649 (loc. 150); no. 2650 (loc. 154).

Family MYRICACEAE

Myrica sonomensis new species

(Plate 37, figures 1, 2)

Description. Leaves lanceolate to oblanceolate; 8.0 cm. long and 2.2 to 2.0 cm. wide; petiole missing; midrib firm and straight; alternate secondaries diverging at variable high angles from the midrib, wavering; irregular tertiaries generally trending at right angles to the secondaries, enclosing an irregular mesh; margin sparsely toothed; texture medium.

Discussion. These leaf impressions are similar to those produced by the living *Myrica californica* Chamisso and Schlechtendal, a bushy tree ranging from Washington southward into southern California. Occurring near the coast throughout its range, it is a common associate of the redwood and north-coast coniferous forests in California.

Many fossil species of *Myrica* have been described from the Cretaceous and Tertiary floras of the northern hemisphere, but most of them are assignable to other genera. *Myrica californica* has been recorded in the Pleistocene of California, but the present occurrence is the first record of a related species in the Tertiary.

Occurrence. Neer's Hill, loc. 154; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2651 (loc. 154); paratype, no. 2652 (loc. 150).

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Family BETULACEAE

Alnus merriami Dorf

(Plate 37, figure 6)

Alnus merriami Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 80–82, pl. 8, figs. 6, 7, 1930.

The only material of *Alnus merriami* that the writer has seen from the Sonoma flora is the specimen figured in this paper, but Dorf reports it from the Matanzas Creek locality. As with the Mulholland specimens discussed in chapter 5 of this volume, it is again evident that *A. merriami* may not be distinct from *A. corrallina* Lesquereux.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2653.

Alnus rubroides new species

(Plate 36, figures 11–13)

Description. Leaves broadest below, exceeding 6.5 cm. in length, and up to 4.0 cm. wide, acute above; petiole missing; firm and heavy midrib; alternate secondaries subparallel, diverging from midrib at 60° to 65° in the lower part of the blade, to as low as 30° in the upper part, ending in marginal teeth, with conspicuous abaxial tertiaries in the outer part which terminate presumably in subsidiary teeth; tertiaries irregularly percurrent, enclosing an irregular polygonal mesh, margin mostly eroded away, but evidently of major rounded and blunt teeth, with subsidiary ones supplied by tertiaries; texture firm.

Cone oblong-ovoid, 1.9 cm. long and 1.7 cm. wide; with a thick stalk.

Discussion. This cone and leaf material of alder from the Neer's Hill locality clearly resembles the modern *Alnus rubra* Bongard (*A. oregona* Nuttall), which ranges from the coastal part of California near Santa Barbara northward into British Columbia. In California it is typically coastal in distribution and is a common species along streams throughout the redwood forest. In more interior and southern localities it mingles with and then is replaced by the more xeric *A. rhombifolia* Nuttall.

Alnus rubroides is distinguishable from *A. merriami* by the fact that the latter species, which is related to the modern *A. rhombifolia,* has a more rounded outline and smaller cones. It differs from *A. relatus* (Knowlton) Brown in that *A. relatus* has a more slender shape and widely spaced subsidiary teeth. *Alnus relatus* has been compared with the modern *A. maritima* Nuttall and *A. japonica* Siebold and Zuccarini, but seems more nearly related to several Mexican species, especially when cone size is also taken into consideration. The type material of *A. carpinoides* Lesquereux differs from *A. rubroides* in the nature of its margin, which is more nearly serrate rather than with rounded coarse teeth.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2654; paratypes, nos. 2655, 2656, 2656*a* (counterpart); no. 2802.

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Family FAGACEAE

Castanea pliocenica new species

(Plate 37, figures 3, 5; plate 39, figure 5)

Ten leaf impressions, none complete, reveal sufficient diagnostic characters to permit the description of a new fossil chestnut.

Description. Leaves lanceolate to oblanceolate, broadest near the middle; 5.0 to 9.0 or 10.0 (estimated) cm. long and 1.8 to 3.0 cm. wide; petiole up to 6 mm. long; midrib strong, straight or slightly curved above; subopposite to alternate secondaries diverging from the midrib at 60° below to as low as 30° in the upper part of the blade, straight or slightly curved, terminating in teeth and commonly on the abaxial side; tertiary veins irregularly percurrent, occasional strong secondaries branching just within the margin; finer nervilles forming a coarse network; teeth dentate, some with short spines; texture coriaceous.

Discussion. This material closely resembles the leaves of the modern *Castanea pumila* Miller, which ranges from New Jersey to Florida and westward into Arkansas and Texas. Among described fossil species, *C. orientalis* Chaney differs from the Sonoma material in its slender shape and greater length. *Castanea castaneaefolia* (Unger) Knowlton from the Latah, which has been considered to represent *C. orientalis* (Brown, 1937*a*, p. 171), is much larger than the Sonoma species. *Castanea lesquereuxi* LaMotte has been considered by Brown (1937*a*) to represent no more than a leaf variation of *Fagus washoensis* LaMotte.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1755; paratypes, nos. 2657, 2681; nos. 2680, 2682.

Castanopsis sonomensis new name

Castanopsis chrysophylloides Lesquereux. Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 90–91, pl. 9, figs. 4, 5, 1930.
LaMotte, Carnegie Inst. Wash. Pub. 455, p. 121, 1936.

The type material of *Castanopsis chrysophylloides* from the Middle Eocene Chalk Bluffs flora has been identified by MacGinitie (1941) as *Tabernaemontana chrysophylloides.* Leaves subsequently referred to *C. chrysophylloides* are definitely referable to *Castanopsis,* as are specimens here noted from the Sonoma flora. They are given the new name *C. sonomensis.*

Description. Leaves lanceolate to long oval; length 4.0 to over 6.0 cm., width 1.4 to 2.2 cm.; bases rounded to obtuse or acute; tips acute to acuminate, but never blunt and rounded; petiole thick, only 4 mm. preserved; midrib straight and heavy; numerous subparallel secondaries diverging at moderate angles, subcamptodrome, occasionally bifurcating near the margin; occasional intersecondaries; tertiaries enclosing a fine, irregular polygonal mesh; margin entire; texture coriaceous.

Discussion. Castanopsis chrysophylla A. DeCandolle, which is closely related to *C. sonomensis,* is a common redwood associate from coast-central California northward to Oregon; from Oregon to Washington it often occurs with the humid north-coast coniferous forest. In recent years it has been found at a few isolated localities in the central Sierra Nevada, where it appears to have survived as a relict from late Tertiary time. Condit's records of *Sequoia* and *Chamaecyparis* in the Mio-Pliocene Remington Hill, as discussed in chapter 2, also indicate a wider distribution of forests containing the Redwood Component during later Tertiary time.

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Castanopsis angustifolia H. V. Smith from the Upper Miocene Thorn Creek flora of southern Idaho has also been compared with the living *C. chrysophylla* (Smith, 1941). One of the specimens of *C. angustifolia* (*ibid.*, pl. 6, fig. 4) may represent a chinquapin of the *chrysophylla* type, but it could also be *Umbellularia*. Of the other specimens, figure 1 on plate 6 is hardly distinguishable from *Sapindus idahoensis* H. V. Smith (*ibid.*, pl. 13, fig. 6). Both of these apparently represent leaves of *Quercus simulata* Knowlton; certainly the leaflets of *Sapindus* do not have petioles 1.5 cm. long. Figure 2 on plate 6 also seems to represent *Quercus simulata;* the character of the secondaries along the margin is totally different from that shown by the modern *Castanopsis chrysophylla,* as may be seen by comparing figure 2 with figure 3 on plate 6. Because there is considerable doubt whether any of these specimens of *Castanopsis angustifolia,* with the possible exception of figure 1, actually represents *Castanopsis,* the writer feels justified in giving the Sonoma material a different name.

Occurrence. Petrified Forest, loc. 150; Matanzas Creek, loc. 152; Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 364 (loc. 154), 365 (loc. 152); nos. 2658, 2659 (loc. 150).

Lithocarpus klamathensis (MacGinitie) new combination

(Plate 37, figure 4)

Quercus klamathensis MacGinitie, Carnegie Inst. Wash. Pub. 416, II, pp. 52–53, pl. 5, fig. 3, 1933.

Lithocarpus predensiflora Brooks, Ann. Carnegie Mus., vol. 24, art. 9, p. 290, pl. 14, fig. 1, 1935.

Pasania densiflora (Hooker and Arnott) Oersted. Hannibal, Bull. Torrey Bot. Club., vol. 38, p. 336, pl. 15, fig. 8, 1911.

Several specimens from the Neer's Hill locality appear to be identical with *Quercus klamathensis* and *Lithocarpus predensiflora.* Both these species show undoubted relationship to the modern tan-bark oak of the Pacific coast, *Lithocarpus densiflora* (Hooker and Arnott) Rehder. Inasmuch as both fossil species have been referred to the same living species, it seems desirable to combine them under the genus to which they are considered related.

Somewhat similar leaves are produced by *Quercus tomentella* Engelmann, whose fossil equivalent, *Q. declinata* Dorf, also occurs in the Sonoma flora. The bases for their differentiation are discussed below under *Q. declinata.*

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2661; no. 2662.

Quercus bockéei Dorf

Quercus bockéei Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 84–86, pl. 9, figs. 1–3, 1930. Condit, Carnegie Inst. Wash. Pub. 553, p. 76, pl. 15, fig. 2, 1944 (see synonymy).

The Petrified Forest is the only locality at which this species has been encountered in the Sonoma formation. Elsewhere it is known from the Mulholland and Table Mountain floras. Its modern affinities are clearly Asiatic, rather than North American, but its exact relationship to any one genus is problematic at this time.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 348, 349, 350; nos. 2663, 2664.

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Quercus convexa Lesquereux

Quercus convexa Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 4, pl. 1, figs. 13–17, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 76, pl. 14, figs. 2, 3, 5, 6, 1944 (see synonymy).

Three nearly complete specimens showing excellent details of venation are exactly like the type material from Table Mountain. Among modern species *Quercus convexa* shows close relationship to *Q. engelmannii* Greene of southern California.

Occurrence. Neer's Hill, loc. 154; Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2665 (loc. 154), 2666 (loc. 152), 2807 (loc. 154).

Quercus declinata Dorf

Quercus declinata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 88–89, pl. 8, fig. 13 (not fig. 12, which is *Q. hannibali* Dorf), 1930.

Axelrod, Carnegie Inst. Wash. Pub. 553, p. 134, 1944 (see synonymy).

Several excellent specimens representing this species were encountered in the recent collections at the Neer's Hill locality. *Quercus declinata* finds its closest modern equivalent in *Q. tomentella* Engelmann of the Channel Islands, off the coast of southern California, and Guadalupe Island. In some cases the leaves of this species bear a superficial resemblance to those of *Lithocarpus.* They may be distinguished by the fact that the secondaries in the leaves of *Lithocarpus* are typically numerous and essentially parallel, whereas leaves of *Q. tomentella* have fewer secondaries, which tend to be wavering and to curve in the outer part of the blade. Another difference is that the tertiaries of *Lithocarpus* are strongly percurrent, whereas in the oak they are irregular.

One of the types of *Quercus declinata* (Dorf, 1930, pl. 8, fig. 12) is in reality *Q. hannibali* Dorf. It differs from *Q. declinata* in its more numerous secondaries, in the character of the tertiaries, and in the teeth.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 357; nos. 2667, 2667*a* (counterpart), 2668, 2669, 2670, 2803.

Quercus douglasoides new species

(Plate 37, figures 7–10)

Quercus orindensis Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 89–90, pl. 9, fig. 7 only, 1930.

Axelrod, Carnegie Inst. Wash. Pub. 476, III, p. 173, pl. 5, fig. 7, 1937.

In our discussion of *Quercus orindensis* on page 135, it was noted that one of the specimens included by Dorf under this species is readily separable from the rest, and is related to the modern *Q. douglasii* Hooker and Arnott. This and other specimens from the Sonoma formation are here described as a new species.

Description. Leaves oval to oblong or obovate, shallowly lobed or coarsely toothed; length 2.2 to 3.7 cm., width 1.2 to 2.0 cm.; petiole stout and short, 2 to 3 mm. long; midrib firm, curved or straight; major secondaries supplying each lobe, commonly 2 to 3, conspicuous intersecondaries between the secondaries, the secondaries diverging at angles from 30° to 85°, often curved either apically or basally, occasionally bifurcating to form a prominent subsecondary, or giving off several strong veins to each of the lobes; coarse teeth enclosing an irregular mesh; the margin

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coarsely toothed or lobed, the lobes often at right angles to one another, each lobe spine-tipped; texture heavy.

Discussion. A dozen specimens of this species, which is closely related to the modern *Quercus douglasii* of California, are represented in the collections from Neer's Hill. The blue oak is a characteristic member of the digger pine forest of central California, and still persists in the Santa Rosa region. North of Santa Rosa its abundance increases as the Coast Range barrier at the west becomes higher, and 20 miles north it is associated with a digger pine forest.

Elsewhere in the western United States, *Q. douglasoides* finds a general relationship to *Q. undulata* Torrey of the southern Rocky Mountains. The Douglasae and Undulatae oaks are not widely separated as to morphological features. That they have largely been distinct since transitional Mio-Pliocene time, however, is suggested by the variation shown by specimens of *Q. douglasoides* in the Remington Hill flora.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 363; plesiotypes, nos. 2671, 2672, 2673, 2801.

Quercus hannibali Dorf

Quercus hannibali Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 86–88, pl. 8, fig. 9 (not figs. 8, 10, which are *Q. wislizenoides* Axelrod, and fig. 11, which is *Photinia sonomensis* Axelrod), 1930.

Axelrod, Carnegie Inst. Wash. Pub. 476, III, p. 173, pl. 5, fig. 6, 1937.

Quercus transgressus Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 59, 1878.

Quercus chrysolepis Liebmann. Hannibal, Bull. Torrey Bot. Club, vol. 38, p. 337, pl. 5, figs. 2, 9, 1911.

Quercus declinata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 88–89, pl. 8, fig. 12 only, 1930.

Quercus traini MacGinitie, Carnegie Inst. Wash. Pub. 416, II, pp. 53–54, pl. 5, figs. 1, 2, 1933.

Brooks, Ann. Carnegie Mus., vol. 24, p. 293, 1935.

H. V. Smith, Papers Mich. Acad. Sci., Arts and Letters, vol. 23, p. 227, 1938.

Quercus browni Brooks, Ann. Carnegie Mus., vol. 24, p. 291, pl. 14, figs. 3–8, 1935.

Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 113, pl. 2, fig. 3, 1936.

Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 98–99, 1939.

H. V. Smith, Papers Mich. Acad. Sci., Arts and Letters, vol. 24, p. 112, pl. 2, figs. 2–4, 6, 1939. Amer. Midland Naturalist, vol. 25, p. 508, pl. 7, fig. 5, 1941.

Odostemon simplex (Newberry) Cockerell. Berry (in part), U. S. Geol. Surv. Prof. Paper 185*e*, pl. 23, fig. 2 only, 1934.

Castanopsis convexa (Lesquereux) Brooks. Dorf (in part), Carnegie Inst. Wash. Pub. 476, II, p. 112, pl. 1, fig. 7 only, 1936.

All the above-listed species closely resemble the modern *Quercus chrysolepis* Liebmann. Variation in individual floras has been noted by the writer, ranging from the large-leafed types, exemplified by the Trout Creek *Q. traini* MacGinitie, to small, sharply serrate leaves which approach the scrub oak, *Q. dispersa* (Lesquereux) Axelrod, in size. As no basis can be found for separating these species, it seems desirable to group all of them under one name.

Quercus transgressus Lesquereux is clearly the oldest species to have been compared to the living *Q. chrysolepis,* but it has not been figured and therefore cannot be evaluated.

Occurrence. Neer's Hill, loc. 154; Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotype, no. 359 (loc. 152); nos. 2660, 2674, 2675 (loc. 154).

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Quercus lakevillensis Dorf

Quercus lakevillensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 82–84, pl. 8, figs. 4, 5, 1930.

Several excellent specimens show that this species is closely related to the modern *Quercus agrifolia* Née, a common California oak. In areas of its northern and coastal distribution it commonly mingles with the redwood forest.

Occurrence. Neer's Hill, loc. 154; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2676, 2677, 2677*a* (counterpart), 2678 (loc. 154), 2679 (loc. 150).

Family ULMACEAE

Ulmus cf. **tanneri** Chaney

(Plate 38, figure 8)

Ulmus tanneri Chaney, Contr. Walker Mus., vol. 2, no. 5, figs. 1, 2, 1920.

A single leaf in the flora closely resembles those produced by the living *Ulmus alata* Michaux of the southeastern United States. Until additional material is obtained, it is referred tentatively to the Lower Miocene Eagle Creek species, which is also related to *U. alata.* The Sonoma specimen is more slender than the types of *U. tanneri,* and narrower in the lower part of the blade. Such variation may readily be seen, however, in the living species. Perhaps the most important difference between the Eagle Creek and Sonoma elms is the smaller size of the Pliocene leaves. Further collections may well show that this feature is sufficiently consistent to provide a basis for specific differentiation, in much the same way as *U. speciosa* differs from *U. californica.*

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2804.

Family NYMPHAEACEAE

Nymphaeites nevadensis (Knowlton) Brown

(Plate 38, figure 2)

Nymphaeites nevadensis (Knowlton) Brown, Jour. Wash. Acad. Sci., vol. 27, p. 509, pl. 1, fig. 10, 1937 (see synonymy).

The characteristic rootstock impressions of this water lily are common in the ashy shales at the Neer's Hill locality. *Nymphaea* occurs today in California in coastal lagoons and in swampy areas within the redwood forest.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2692; nos. 2693, 2694, 2695.

Family BERBERIDACEAE

Mahonia hollicki (Dorf) Arnold

Mahonia hollicki (Dorf) Arnold, Contr. Mus. Paleontol. Univ. Mich., vol. 5, no. 4, p. 61 (not pl. 2, figs. 3–8, and pl. 3, figs. 5, 7, 9, which are *M. reticulata* (MacGinitie) Brown), 1936.

Odostemon hollicki Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 93–94, pl. 10, figs. 7, 8, 1930.

Although Arnold has considered the Trout Creek material to be similar to the California Pliocene species, Brown (1937*a*, p. 175) has indicated that they are distinct.

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Mahonia hollicki, which shows relationship to the modern *M. aquifolium* Pursh, was not encountered in the recent collection.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 370, 371.

Mahonia prelanceolata Condit

Mahonia prelanceolata Condit, Carnegie Inst. Wash. Pub. 553, pp. 77–78, pl. 15, fig. 3, 1944.

The basal two-thirds of a leaflet in the Sonoma flora is indistinguishable from the Table Mountain *Mahonia prelanceolata.* All the specimens are closely similar to leaflets of the living *M. lanceolata* Fedde of northern Mexico. It is of considerable interest that 2 other species in the Sonoma flora, *Ilex sonomensis* and *Persea coalingensis,* find their nearest living counterparts in the pine-oak country of the Sierra Madre Occidental in close proximity to *M. lanceolata.*

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2808.

Mahonia simplex (Newberry) Arnold

Mahonia simplex (Newberry) Arnold, Contr. Mus. Paleontol. Univ. Mich., vol. 5, no. 4, p. 58, pl. 1, figs. 1–3, 6, 7; pl. 2, figs. 1, 2, 1936 (see synonymy).
Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 175, 1937 (see synonymy).

The upper half of a leaflet from the Neer's Hill locality seems to be indistinguishable from the figured specimens representing this species, with which it is tentatively compared. Among living members of the genus, such Asiatic species as *Mahonia beali* Carrière and *M. japonica* DeCandolle resemble *M. simplex.*

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2683.

Family LAURACEAE

Persea coalingensis (Dorf) Axelrod

(Plate 38, figures 1, 3)

Persea coalingensis (Dorf) Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 131–132, 1944 (see synonymy and discussion).

The leaves of *Persea* have been collected at the three Sonoma plant localities. The slender shape of the Sonoma, Tehachapi, and San Joaquin specimens seems to relate *P. coalingensis* more nearly to the Mexican *P. podadenia* Blake than to any other American species.

Occurrence. Petrified Forest, loc. 150; Matanzas Creek, loc. 152; Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2684, 2685 (loc. 154); nos. 2686, 2687, 2688 (loc. 150), 2689 (loc. 152).

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939 (see synonymy).

Leaves of the California laurel, *Umbellularia californica* Nuttall, are represented by well preserved specimens of *U. salicifolia* in the collections from the Neer's Hill and Petrified Forest localities.

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Occurrence. Petrified Forest, loc. 150; Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 372 (loc. 150), 2690, 2690*a* (counterpart), 2691 (loc. 154).

Family PLATANACEAE

Platanus paucidentata Dorf

Platanus paucidentata Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 94–96, pl. 10, figs. 4, 9; pl. 11, fig. 1; pl. 12, fig. 1, 1930.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 48–49, pl. 9; pl. 10, fig. 4; pl. 11, fig. 5, 1944 (see synonymy).

Battered sycamore leaves apparently transported for some distance to the site of deposition are not uncommon in the Neer's Hill and Matanzas Creek collections. The suggestion that sycamore did not live at these immediate localities is consistent with the belief that members of the border-redwood forest lived on leeward slopes and in more exposed areas bordering the mesic coastal valley which extended into the Santa Rosa region during Sonoma time.

Although the sycamore leaves in the Sonoma flora have been assigned to this Pliocene species, it must be pointed out that characters diagnostic of any one species are not shown by these battered specimens. In view of the general character of the flora, it would not be surprising to find that they represent *Platanus dissecta* or *P. aceroides.*

Occurrence. Matanzas Creek, loc. 152; Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 377, 378 (loc. 152); nos. 2696 (loc. 152), 2697 (loc. 154).

Family ROSACEAE

Photinia sonomensis Axelrod

Photinia sonomensis Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 139–140, 1944 (see synonymy and discussion).

Only a part of a leaf representing this species, which was originally collected at the Petrified Forest, has been encountered in the recent collections. It shows an undoubted relationship to the modern toyon, *Photinia arbutifolia* Lindley, which is a common shrub at the locality today.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 390; no. 2698.

Family LEGUMINOSAE

Amorpha condoni Chaney

(Plate 38, figure 4)

Amorpha condoni Chaney, Carnegie Inst. Wash. Pub. 553, pp. 318–319, pl. 51, figs. 2–4, 1944.

Ten excellent specimens resemble in all details the leaflets produced by the modern mock locust of California, *Amorpha californica* Nuttall. In the more northern parts of its range, *Amorpha* is common in the border-redwood forest.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2699, 2699*a* (counterpart); no. 2809.

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Family AQUIFOLIACEAE

Ilex sonomensis Dorf

(Plate 38, figure 9)

Ilex sonomensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 101–103, pl. 12, figs. 6, 7; pl. 13, figs. 1, 2, 1930.

Leaves representing this species are particularly abundant at the Petrified Forest locality. Among modern species a general relationship is apparent with *Ilex brandegeana* Loesener of northern Mexico.

Occurrence. Petrified Forest, loc. 150; Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 396, 397, 398, 399 (loc. 150); plesiotype, no. 2700 (loc. 150); no. 2701 (loc. 152).

Family RHAMNACEAE

Ceanothus precuneatus Axelrod

Ceanothus precuneatus Axelrod, Carnegie Inst. Wash. Pub. 516, p. 120, pl. 11, fig. 7, 1939.

The basal two-thirds of a leaf and its counterpart reveal all the essential characters of this species, which is considered to be closely related to the modern *Ceanothus cuneatus* Nuttall of California. The fossil specimen is somewhat larger than those produced by the modern species in areas of its southern distribution, but is nearly identical with those collected from areas near the redwood forest in the north Coast Ranges.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2702, 2702*a* (counterpart).

Ceanothus sp.

(Plate 38, figure 7)

This fragmentary specimen is distinct from the several described species of *Ceanothus* in the Tertiary of western North America. Among modern plants it shows general relationship to the smaller leaves produced by *C. thyrsiflorus* Eschscholtz of coastal California. Specimens collected by the writer in the redwood forest at Fort Bragg duplicate in all details the characters revealed by the fossil species.

Ceanothus blakei Chaney from the Bridge Creek flora has been compared with *C. thyrsiflorus,* but it differs from the living species in having an ovate shape and a serrulate margin. In the genus *Ceanothus, C. blakei* more nearly resembles *C. velutinus* Douglas than *C. thyrsiflorus.* It also shows a general resemblance to *Paliurus,* and is only slightly smaller than the Latah *P. hesperius* Berry.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2703.

Rhamnus idahoensis Brown

Rhamnus idahoensis Brown, Jour. Paleontol., vol. 9, p. 581, pl. 69, fig. 13, 1935. U. S. Geol. Surv. Prof. Paper 186*j*, p. 181, pl. 56, fig. 4, 1937.

Two fragments representing comparatively large leaves, with percurrent venation and finely serrate or entire margin, are sufficiently well preserved to reveal the typical features of *Rhamnus,* and to indicate that they are related to the modern *R. purshiana* DeCandolle of the Pacific states. In California this species ranges southward into

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the coastal parts of Mendocino County, where it is a common member of the redwood forest.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2704, 2704*a* (counterpart), 2806.

Family HYDROCARYACEAE

Trapa americana Knowlton

(Plate 39, figures 1, 4)

Trapa americana Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 733, pl. 102, fig. 7*a*, 1898.

Berry, Proc. U. S. Nat. Mus., vol. 72, art. 23, p. 13, pl. 2, figs. 5, 6, 1927.

Brown, Jour. Paleontol., vol. 9, no. 7, p. 581, pl. 67, fig. 17, 1935. U. S. Geol. Surv. Prof. Paper 186*j*, p. 183, pl. 55, figs. 5, 6, 1937.

Trapa ? occidentalis Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 734, pl. 102, fig. 7*b*, 1898.

Trapa prenatans Dorf, Carnegie Inst. Wash. Pub. 476, II, pp. 122–123, pl. 3, fig. 6, 1936.

The writer has had opportunity to examine all species listed in the above synonymy, which already has been proposed by Brown (1935, 1937*a*), and it is clear that all of them represent a 4-horned species of *Trapa*. Leaves of this species have been collected recently by the writer at Coal Valley, Nevada, where the fruits of *T. americana* are particularly abundant, and they closely resemble those produced by the modern *T. natans* Linnaeus.

Fruits of *Trapa americana* are relatively abundant at the Neer's Hill locality. One of them (pl. 39, fig. 4) is a 2-horned fruit resembling those produced by the modern *T. bicornis* Linnaeus, but until additional material of this kind can be obtained, it seems best to regard it as a variant of *T. americana*. It may be noted that the modern *T. bicornis* is considered by certain authors to represent only a form of *T. natans*.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2705, 2706, 2706*a* (counterpart); nos. 2707, 2707*a* (counterpart), 2708, 2709.

Family CORNACEAE

Garrya masoni Dorf

(Plate 39, figures 6, 7)

Garrya masoni Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 104–106, pl. 13, fig. 5, 1930.

Several specimens of *Garrya* were encountered in the recent collections at the Petrified Forest. The Sonoma material differs from *Garrya masoni* in the nature of the margin, which is entire in the Sonoma specimens, and revolute and undulate in the Coalinga specimen. It must be noted, however, that the modern species which resemble the fossils most closely, *G. elliptica* Douglas and *G. fremontii* Torrey, may produce leaves of both types. In areas of its more mesic distribution, *Garrya* commonly produces entire rather than undulate or revolute leaves. These latter leaf forms are found typically in the more semiarid parts of its range. In view of the mesic aspect of the associated flora, it is to be expected that the leaves of *G. masoni* at Sonoma would be of the entire rather than of the undulate type.

Occurrence. Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2710, 2711.

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Family ERICACEAE

Rhododendron sp.

(Plate 39, figures 2, 3)

Rhododendron californicum Hooker is a regular associate of the redwood forest on the north coast of California, but its fossil equivalent has not been recorded in the Arcto-Tertiary Flora of the western United States. Four leaf bases in the Neer's Hill florule show close relationship to *R. californicum,* but are too incomplete to warrant description as a fossil species.

Leaves apparently long elliptical in outline, tapering to a long-acute base; total length unknown but certainly exceeding 7.0 cm.; width 3.0 cm. and more; petiole thick and heavy, up to 1.0 cm. preserved; thin alternate secondaries diverging from the midrib at moderate to high angles, looping upward along the margin, camptodrome; thin intersecondaries; tertiaries enclosing a coarse and quadrangular mesh; margin entire; texture thick.

Rhododendron californicum ranges from Washington southward into California with the redwood forest, and is clearly an indicator of mesic conditions. At the south it is limited largely to seaward-facing canyons in the redwood forest, but northward it ranges inland with the forest where rainfall is heavy and fogs are frequent.

Many fossil species of *Rhododendron* have been described from the Tertiary of Europe, but *R. sierrae* Condit from the Table Mountain flora and the present specimens comprise the only described records of the genus in the Tertiary of western North America. The Table Mountain species, which has Asiatic rather than American affinities, differs from the Sonoma species in its long, slender outline. *Rhododendron idahoensis* H. V. Smith (1939) from Thorn Creek apparently is fagaceous; its venation is totally different from that shown by *Rhododendron.* One of the Thorn Creek species, however, *Arbutus opaca* H. V. Smith (1941), may be *Rhododendron;* judging from the figure and the description, it compares closely with the modern *R. californicum.*

The high concentration of *Rhododendron* species in China today suggests that the modern American species of the genus may be relicts of the element now restricted to Asia (*Cercidiphyllum, Ginkgo, Glyptostrobus, Koelreuteria, Pseudolarix, Trapa*) which was abundant at middle latitudes in North America during the Middle Tertiary. *Castanopsis* and *Lithocarpus* probably are to be interpreted similarly.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2712, 2713, 2713*a* (counterpart), 2714, 2714*a* (counterpart), 2805.

Vaccinium sonomensis new species

(Plate 38, figures 5, 6)

Description. Leaves lanceolate to oval; 1.5 cm. long and 4 to 6 mm. wide; petiole slender; midrib firm and straight; alternate secondaries diverging at moderate to low angles, camptodrome along the margin; tertiaries irregular; occasional intersecondaries, short and joining with the secondaries in the middle of the blade; margin entire; texture medium.

Discussion. These specimens of *Vaccinium* from the Neer's Hill and Petrified Forest localities are clearly related to the modern *V. parvifolium* Smith, which ranges

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with the redwood forest from the Santa Cruz Mountains northward, and occurs also in the Sierra Nevada and thence northward along the Pacific coast to Alaska.

Among the Tertiary species of *Vaccinium* in the western United States, *V. sonomensis* is most nearly like *V. bonseri serrulatum* Berry from the Latah and Thunder Mountain floras, but differs from that species in having an entire rather than a serrate margin. *Vaccinium bonseri* Berry appears to be identical with *Arctostaphylos cuneata* Brown.

Occurrence. Neer's Hill, loc. 154; Petrified Forest, loc. 150.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, nos. 2715, 2715*a* (counterpart) (loc. 154); paratype, no. 2716 (loc. 150).

Family OLEACEAE

Fraxinus caudata Dorf

Fraxinus caudata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 106–107, pl. 13, fig. 8 (not figs. 6, 7, which are *Persea coalingensis* (Dorf) Axelrod), 1930.

Two specimens showing excellent details of venation are indistinguishable from the leaflets produced by the modern *Fraxinus oregona* Nuttall of the Pacific coast. The modern species is common along streams in the more open parts of the redwood forest in California, particularly from the San Francisco Bay region northward.

Occurrence. Neer's Hill, loc. 154; Matanzas Creek, loc. 152.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2717 (loc. 154), 2718 (loc. 152).

Family CAPRIFOLIACEAE

Symphoricarpos salmonensis Brown

Symphoricarpos salmonensis Brown, Jour. Paleontol., vol. 9, no. 7, p. 583, pl. 69, fig. 7, 1935.

A specimen and its counterpart reveal all the characteristic features of this genus, and cannot be differentiated from the type material. The Sonoma species shows close relationship to the modern *Symphoricarpos albus* Blake, a common shrub in the general region of the fossil locality today.

Occurrence. Neer's Hill, loc. 154.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2719, 2719*a* (counterpart).

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PLATES 34—39

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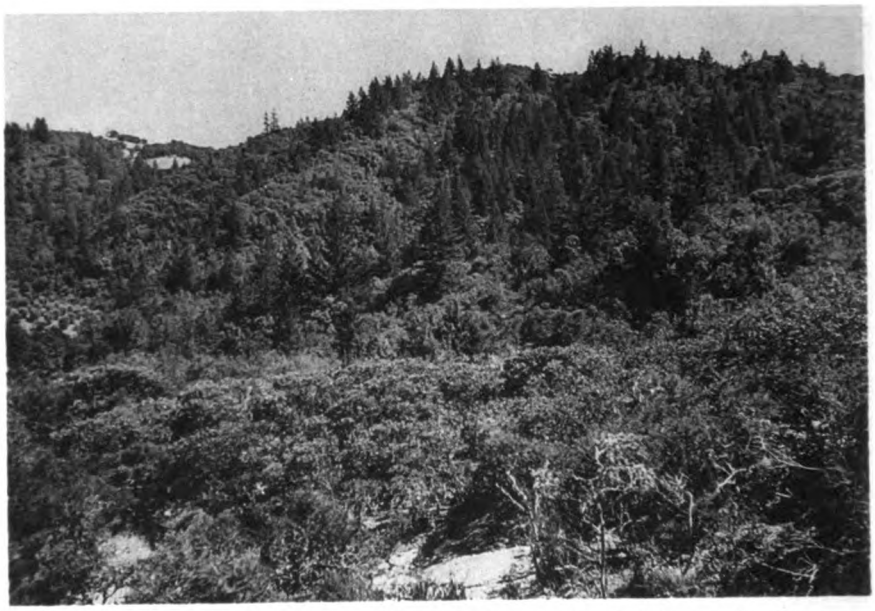

FIG. 1. Border-redwood forest and chaparral near Petrified Forest, locality 150

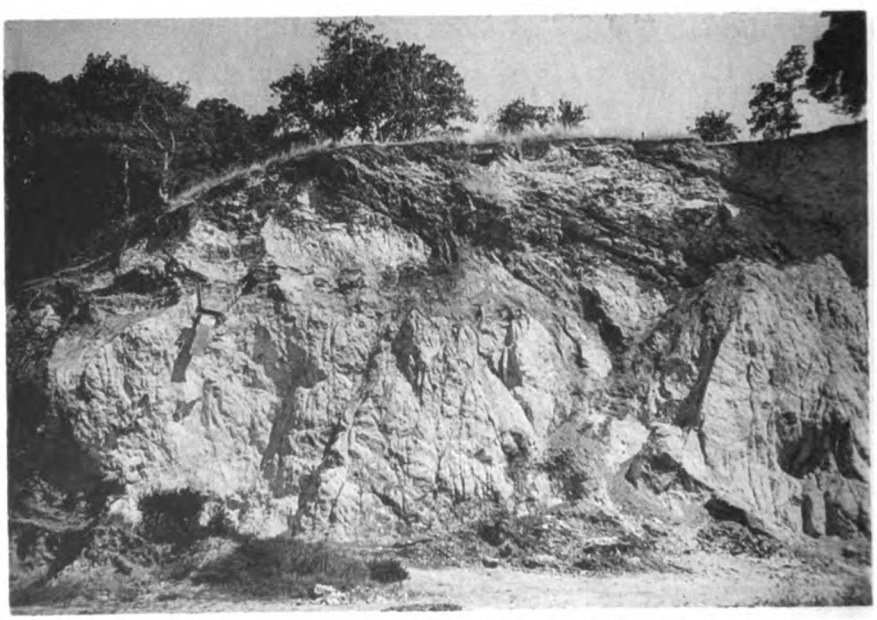

FIG. 2. Exposure of Sonoma tuff at Neer's Hill, locality 154

SONOMA LOCALITY AND MODERN VEGETATION

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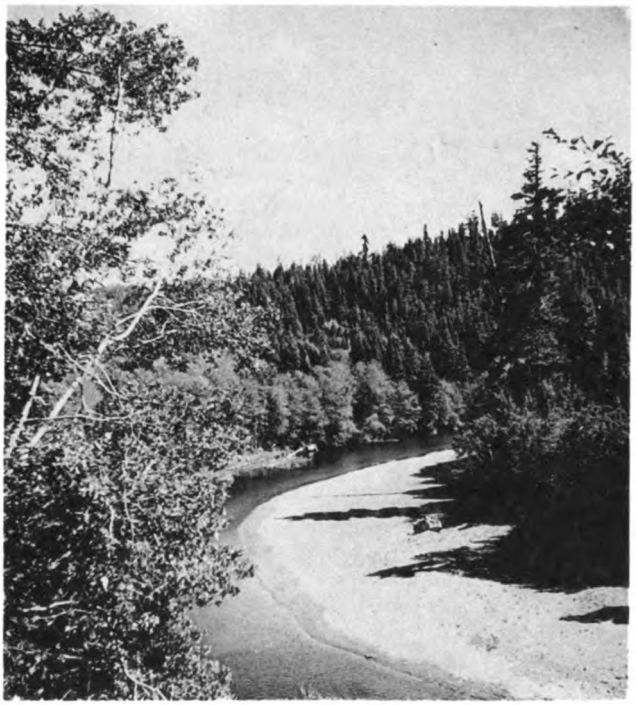

FIG. 1. Interior of the coast forest. Association of *Pseudotsuga taxifolia, Sequoia sempervirens, Abies grandis,* and *Tsuga heterophylla* near southern limit of north-coast coniferous forest, Gualala River.

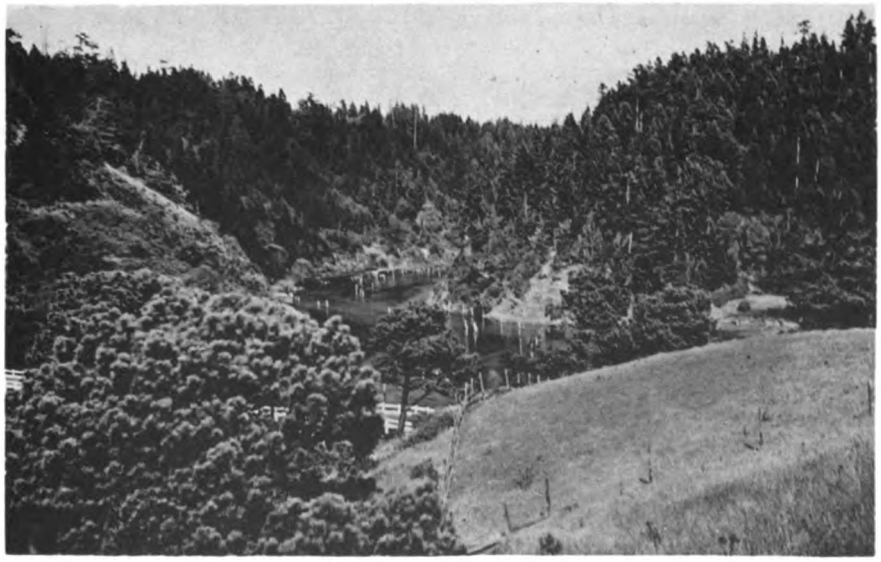

FIG. 2. Coast forest near Fort Bragg, California. Coastal conifer forest on river slopes, with closed-cone pine forest in foreground.

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PLATE 36

SONOMA FOSSILS

PAGE

FIG. 1. *Cupressus sonomensis* Axelrod. Holotype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 2640 192

FIG. 2. *Picea sonomensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2631 190

FIG. 3. *Pseudotsuga sonomensis* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2632 191

FIG. 4. *Abies sonomensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2624 190

FIG. 5. *Tsuga sonomensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2634 192

FIG. 6. *Tsuga sonomensis* Axelrod. Paratype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 2635 192

FIG. 7. *Abies sonomensis* Axelrod. Paratype. U. C. Mus. Pal., Paleobot. Ser., no. 2625 190

FIGS. 8–10. *Salix boisiensis* H. V. Smith. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2648, 2646, 2647 194

FIG. 11. *Alnus rubroides* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2654 195

FIGS. 12, 13. *Alnus rubroides* Axelrod. Paratypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2656, 2655 195

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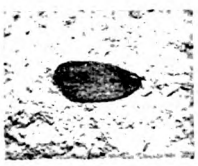

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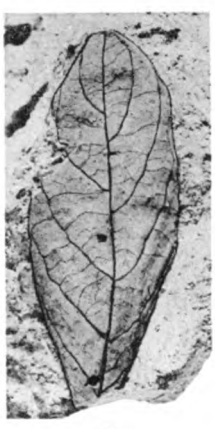

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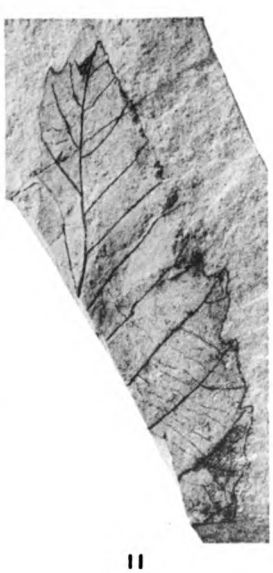

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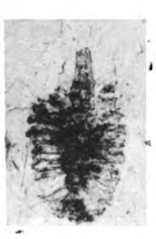

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PLATE 37

Sonoma fossils

PAGE

Fig. 1. *Myrica sonomensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2651 194

Fig. 2. *Myrica sonomensis* Axelrod. Paratype. U. C. Mus. Pal., Paleobot. Ser., no. 2652 194

Figs. 3, 5. *Castanea pliocenica* Axelrod. Paratypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2657, 2681 196

Fig. 4. *Lithocarpus klamathensis* (MacGinitie) Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2661 197

Fig. 6. *Alnus merriami* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2653 195

Figs. 7–10. *Quercus douglasoides* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2672, 2671, 2801, 2673 198

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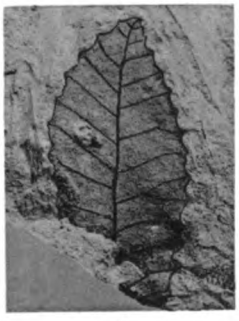

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PLATE 38

Sonoma fossils

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Figs. 1, 3. *Persea coalingensis* (Dorf) Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2685, 2684 201

Fig. 2. *Nymphaeites nevadensis* (Knowlton) Brown. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2692 200

Fig. 4. *Amorpha condoni* Chaney. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2699 202

Fig. 5. *Vaccinium sonomensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2715 205

Fig. 6. *Vaccinium sonomensis* Axelrod. Paratype. U. C. Mus. Pal., Paleobot. Ser., no. 2716 205

Fig. 7. *Ceanothus* sp. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 2703 . . 203

Fig. 8. *Ulmus* cf. *tanneri* Chaney. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2804 200

Fig. 9. *Ilex sonomensis* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2700 203

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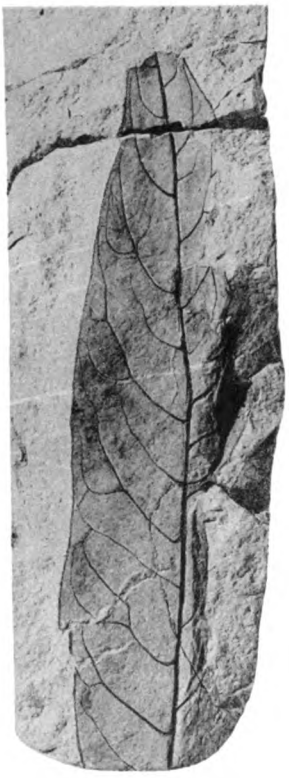

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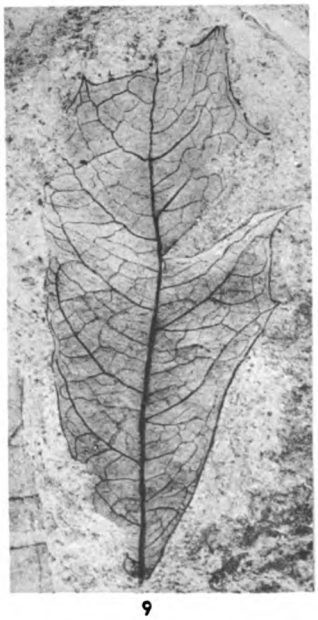

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PLATE 39

SONOMA FOSSILS

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FIGS. 1, 4. *Trapa americana* Knowlton. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2706, 2705 204

FIGS. 2, 3. *Rhododendron* sp. U. C. Mus. Pal., Paleobot. Ser., nos. 2713, 2712 205

FIG. 5. *Castanea pliocenica* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1755 196

FIGS. 6, 7. *Garrya masoni* Dorf. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2711, 2710 204

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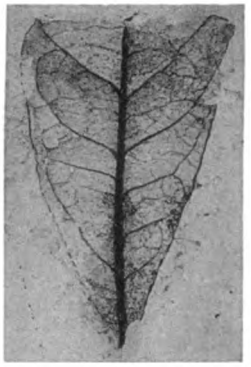

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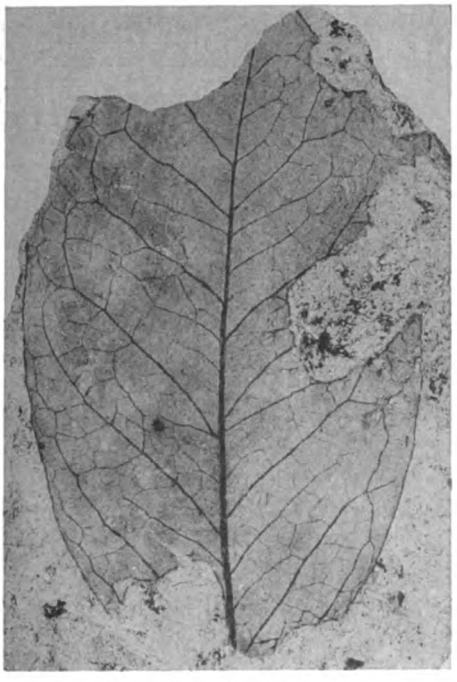

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8

The Pliocene Sequence in Central California

DANIEL I. AXELROD

Introduction

In the case of Tertiary floras whose stratigraphic position is not clearly defined, the major basis for age determination lies in a recognition of the changes in distribution and composition of the successive floras (Chaney, 1936*a*, 1936*b*, 1940). Through the Tertiary there is evidence of gradual modification in composition and distribution in response to a trend from warm and moist climate early in the period to cooler and drier conditions later in the series. Homogeneous forests, at the outset widely distributed over regions of low to moderate relief, gave place to diversified units controlled by local climate and topography. Although the floras of the four epochs may be differentiated by this method, and the subdivisions of the Eocene, Oligocene, and Miocene may be distinguished in most cases, the task of placing a Pliocene flora in any part of that stage has until recently proved difficult or impossible. This has been due to at least two major difficulties (Axelrod, 1938): (1) Pliocene floras are highly localized in development and are difficult to correlate over wide areas, and (2) no climatically sensitive group of plants has previously been recognized that would afford a basis for correlation between these floras.

Intensive studies of Pliocene floras in the western United States during the past few years have convinced the writer that the difficulties of Pliocene correlation may be overcome by recognizing three facts. In the first place, there are five climatically sensitive groups of plants which may be used in age determination. The first consists of relict members of the East American and East Asian Elements which survived into the Pliocene. These include such genera as *Carya, Castanea, Nyssa, Ostrya, Trapa,* and *Ulmus,* and also certain species of *Alnus, Populus, Quercus,* and *Rhododendron.* The second group includes members of the West American Element recorded in areas now geographically remote from those where their nearest modern descendants are found. These may be grouped into five components, the Redwood, North-coast coniferous, Sierra-Cascade, Rocky Mountain, and Border-redwood. With increasing aridity, members of these components, which are listed above largely in order of decreasing mesophytism, will disappear from any province essentially in the order given. The third group of climatic importance comprises members of the Southwest American Element which now have their nearest relatives in the southwestern United States and northern Mexico. They have been recorded from the later Tertiary in California, the Great Basin, the Columbia Plateau, the Colorado Plateau, and the High Plains. Belonging to this group are such genera as *Ilex, Robinia, Sapindus,* and *Ungnadia,* in addition to certain species of *Arbutus,*

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Cercocarpus, Mahonia, Populus, Quercus, and *Rhus.* The fourth group having definite climatic significance in the Pliocene includes members of the Southwest American Element that have survived down to the present at the north, but persist in regions geographically remote from the fossils most nearly related to them. Here may be cited the occurrence of relatives of typical southern California species in central California, for example *Lyonothamnus mohavensis, Quercus declinata,* and *Rhus moragensis;* or such California plants in central Nevada and southern Oregon as *Arctostaphylos, Ceanothus, Cercocarpus,* and *Quercus.* Finally, the fifth group having real climatic value in the later Tertiary is represented by species with leaves of smaller size and thicker texture than their nearest fossil relatives. Both the Miocene and the Pliocene species, which are distributed among such genera as *Acer, Amelanchier, Arbutus, Populus, Rosa,* and *Ulmus,* are related to the same modern species. A Miocene poplar, for example, most nearly resembles the leaves produced by its modern equivalent in the humid parts of its range; the Pliocene is more nearly like the smaller and thicker-textured leaves produced by the same species in the arid parts of its distribution (Chaney, 1938*a*; Axelrod, 1941).

With the recognition of these five groups having climatic importance in later Tertiary floras, the second fact to be noted in Pliocene correlation is that the succession of Pliocene vegetation differs greatly in the several paleobotanical provinces. It is therefore necessary in evaluating these climatically sensitive groups to establish for each province the time of their appearance, optimum development, and disappearance. For example, the East American and East Asian Elements are known to have survived into the Upper Pliocene in west-central California near the coast, but they disappeared from west-central Nevada in the Lower Pliocene. The Southwest American Element dominated the Mohave region during Middle Miocene time, but does not appear as an important group in the foothill region on the windward slopes of the central Sierra Nevada until the end of that epoch, or in west-central California until the later part of Lower Pliocene time. Likewise, a small-leafed "Pliocene" species such as *Populus pliotremuloides* may occur in the western Mohave area in the early Miocene, because semiarid conditions had appeared there by that time. But this species does not appear in the Columbia Plateau until Pliocene time, because semiarid climate did not develop there until early in that epoch.

This concept of a different floral sequence in the several provinces leads directly to the third factor which must be considered in establishing the age of a Pliocene flora. Correlation cannot be made between the different provinces on the basis of specific relationships. The time of development and disappearance of the floristic elements varies from province to province, depending on position with respect to the ocean and to the leeward and windward slopes of mountain ranges, as well as with respect to elevation and latitude. In the later Tertiary there has been recorded a northward and coastward movement, in a general fan-wise manner, of semiarid interior vegetation which gradually replaced mesic forests of northern derivation. Thus any close specific resemblance between

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floras of two provinces at different latitudes must indicate a difference in age. In this connection it may be noted that Chaney has recently commented upon the idea of homotaxis and synchronism as follows (1940, p. 476):

> Applying the concept of homotaxis to problems of Tertiary correlation, it seems clear that floral and faunal resemblances across a wide range of latitude may be an indication not of contemporaneity but of discrepancies in age. Correlation of plant-bearing beds in western America is always subject to this application of the time-space concept. As our knowledge of the stratigraphic and geographic distribution of fossil floras increases, we shall be able to evaluate still more closely the time factor in plant migrations.

It is evident also that floras of similar composition at the same latitude and altitude but occupying different positions with respect to the ocean or mountain ranges may also be of different age; for mesic elements disappear first from interior regions, and persist for a longer time on windward slopes and near the ocean.

Thus an evaluation of the time factor during the Pliocene must be made on the basis of an established floristic and climatic trend in each of the several provinces. Attempts at interprovincial correlation by the percentage method will result only in confusion. It is therefore necessary to determine first as completely as possible the later Tertiary floristic sequence in the several provinces of the western United States. Only then will it be possible to show that such dissimilar floras as the desert-border Ricardo and the hardwood-deciduous Black Hawk Ranch assemblages are essentially contemporaneous.

This discussion of the floristic sequence in central California forms the first of several summary papers which will be directed toward recording the Pliocene paleobotanical sequence in the western provinces of the United States. It is fully realized that the data now available are incomplete, and that the discovery of additional floras may provide evidence necessitating modification of certain interpretations. Nevertheless, the following sections of this chapter are believed to outline the essential features of the floral sequence in central California during Pliocene time, and to add materially to an understanding of this latest but most diversified epoch of the Tertiary. The floras to be discussed are grouped in table 20 according to their relative ages; associated vertebrate and invertebrate faunas are also included.

West-Central California

In the following discussion of the floristic sequence in west-central California, seven floras ranging in age from latest Miocene (or Mio-Pliocene transition) to late Upper Pliocene will be considered. These are arranged according to their relative ages in table 20 and will be discussed in order, commencing with the oldest. One of these floras, the Diablo, has not been previously described, but it is of sufficient importance to be alluded to briefly.

The Neroly flora of the Mount Diablo region represents a *Taxodium-Nyssa*

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TABLE 20

RELATIVE AGES OF THE LATER TERTIARY FLORAS OF CENTRAL CALIFORNIA, AND THEIR ASSOCIATED VERTEBRATE AND INVERTEBRATE FAUNAS

STAGE	WEST-CENTRAL CALIFORNIA	CENTRAL SIERRA NEVADA	ASSOCIATED VERTEBRATE* AND INVERTEBRATE† FAUNAS
UPPER PLIOCENE	Santa Clara		
	Sonoma		"Merced"†
MIDDLE PLIOCENE	Petaluma	Oakdale	Petaluma* Oakdale*
	Mulholland		Mulholland*
LOWER PLIOCENE	Black Hawk Ranch		Black Hawk Ranch*
	Diablo		Diablo†
	Neroly	Table Mountain	Springfield Shaft*
		Remington Hill; Mohawk	Neroly*†
UPPER MIOCENE		Valley Springs	

community whose associates include many of the fossil equivalents of the regular members of that forest now surviving in the eastern United States (Condit, 1938):

Berchemia	Juglans	Populus
Betula	Magnolia	Prunus
Chionanthus	Myrica	Smilax
Ilex	Platanus	

In addition to these, there is a smaller number of plants, represented by such genera as *Alnus, Populus,* and *Umbellularia,* whose nearest modern descendants now survive in California. A third group includes species of *Myrtus, Persea,* and *Tetracera* which are considered to be relicts of earlier Tertiary vegetation and to represent the Caribbean Element. Condit has pointed out that the flora as a whole suggests conditions near the borders of the typical *Taxodium* forest, rather than in regions of its optimum development (1938, p. 238). The Neroly flora apparently was laid down along a flood plain and on the shores of a

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marine embayment which extended into the Mount Diablo area in Neroly time. It has been pointed out that this coastal plain probably was continuous eastward into the foothills of the Sierra Nevada, the region from which it appears to have derived some of its sediments (Louderback, 1924; Condit, 1938, p. 230). An annual rainfall of 40 to 45 inches has been suggested for the Neroly climate, but

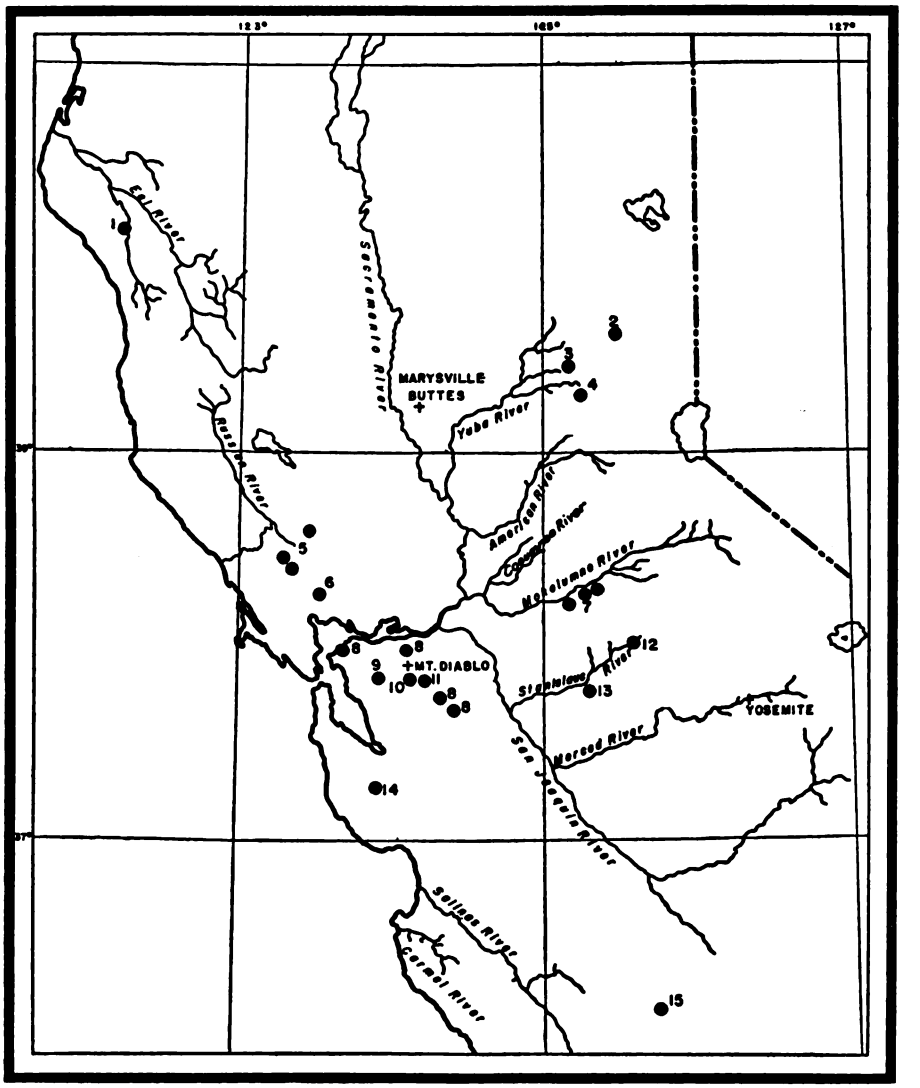

FIG. 3. Mio-Pliocene and Pliocene plant localities in central and northern California.

1. Wildcat
2. Mohawk
3. Forest
4. Remington Hill
5. Sonoma
6. Petaluma
7. Valley Springs
8. Neroly
9. Mulholland
10. Black Hawk Ranch
11. Diablo
12. Table Mountain
13. Oakdale
14. Santa Clara
15. San Joaquin

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it may be that precipitation was as low as 35 inches yearly. The bald cypress (*Taxodium distichum* Richard) of the eastern United States ranges into areas where rainfall reaches this minimum, and *T. mucronatum* Tenore occupies stream banks in the deserts of central and northern Mexico. This suggestion of a somewhat lower rainfall for the Neroly flora is supported by the differences between the coastal and inland florules. Those from the interior, at Altamont Pass and Corral Hollow, are largely riparian in aspect, whereas the Loma Ranch florule, north of Mount Diablo, suggests a denser forest cover, such as would be expected near the coast where conditions were more moderate. Furthermore, species of common occurrence in interior localities, such as *Alnus corrallina,* are less abundant near the coast, whereas the common coastal species such as *Taxodium dubium* and *Nyssa knowltoni* are rare in the interior. This distribution suggests lower rainfall and greater extremes of temperature at the interior. In this connection it may be noted that the writer has recently collected a small florule from rhyolite ash below a typical Neroly flora in the Corral Hollow region. It contains an abundance of *Quercus hannibali* leaves, several specimens of *Quercus prelobata,* and such typical Neroly plants as *Taxodium dubium* and *Persea pseudo-carolinensis.* Although these oaks have not been recorded in the Neroly flora (Condit, 1938, pp. 233–234), there is a specimen of *Quercus convexa* in the collection at the U. S. National Museum from Corral Hollow. This indication of a drier climate at the interior is consistent also with the semiarid aspect of the Table Mountain flora, which is of essentially the same age and lies in the foothills of the Sierra Nevada 70 miles east (chap. 3 above).

Rainfall during Neroly time may have been distributed rather evenly throughout the year, but an examination of the transitional Mio-Pliocene Table Mountain (chap. 3) and the Upper Miocene Valley Springs floras (see pages 217–220) to the east in the central Sierra Nevada, and the Upper Miocene Puente (Axelrod, 1939, pp. 56, 68), Mint Canyon (Axelrod, 1940*c*), and Monterey floras to the south, suggests that it may have been biseasonal in occurrence. These floras indicate such a condition, and there is no apparent reason for assuming that it did not extend also over the Neroly area. The northward movement of the semiarid Madro-Tertiary Flora into these localities is clearly an expression of changing conditions in the north during the late Upper Miocene. Since members of this semiarid flora lived in the western Mohave area during early Middle Miocene time under biseasonal precipitation (Axelrod, 1939), it seems reasonable to believe that their appearance at the north was due to the northward expansion of a drier climate. The rarity of arid southern plants in the lowland Neroly flora seems explainable on the basis of the edaphic conditions demanded by flood-plain vegetation. Plants requiring drier soils would be found growing on adjacent hills away from immediate sites of Neroly deposition.

The general floristic and climatic conditions in west-central California at the close of the Miocene which have a bearing on the interpretation of Pliocene floras are as follows: In the Mount Diablo area and near the borders of the Neroly embayment, a relict *Taxodium-Nyssa* community persisted under an

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annual rainfall of 35 inches or more. The rainfall may have been distributed biseasonally, and near the coast such factors as a low evaporation rate, moderating maritime conditions, and a high water table throughout the year were operative. Some of the characteristic flood-plain members of this community extended across the Great Valley and into the foothills of the Sierra Nevada, where they are represented in the Mio-Pliocene floras of that region; these will be more fully discussed in the next section of this chapter. In this easterly area, where extremes of temperature were greater and the compensatory factors found along the coast were less effective, mesic species have a more limited occurrence, and members of the semiarid Madro-Tertiary Flora are increasingly numerous.

Floristic modifications following the Neroly in west-central California seem related to the general trend to aridity in western America at that time, as well as to changing paleogeographic features which modified climatic and edaphic conditions in lowland areas where plants were accumulating. The beds succeeding the Neroly on the southwestern slopes of Mount Diablo contain a marine fauna showing affinities with the Lower Pliocene Jacalitos (Clark, 1935, p. 1035). This formation has been termed the Alamo by Clark (1940). Since the name is preoccupied, it is here renamed the *Diablo formation* for the excellent exposures in the area near the Diablo post office. A well preserved flora occurs in brown, semi-cherty mudstones near the base of this Diablo formation. Preliminary work on the Diablo collections shows that this early Pliocene flora is dominated by *Persea pseudo-carolinensis* Lesquereux and *Betula vera* Brown, with associates of *Platanus dissecta* Lesquereux, *Smilax diforma* Condit, *Ulmus* cf. *tanneri* Chaney, and *Umbellularia salicifolia* (Lesquereux) Axelrod. The Diablo differs from the Neroly flora 12 miles north in that it lacks the dominant *Taxodium-Nyssa* community of that flora. Whereas the Diablo suggests conditions somewhat cooler and slightly drier than those of Neroly time, in its abundance of *Persea* and absence of semiarid species of the Southwest American Element it indicates a warmer and moister climate than that of the following Black Hawk Ranch stage.

The Diablo formation grades upward into continental sediments containing the Black Hawk Ranch fauna and flora (chap. 4). There is evidence of the presence during this stage of a low range at the site of Las Trampas Ridge 5 miles to the west.[1] The elevation of this barrier apparently caused a climatic change sufficient to eliminate many of the mesic Neroly genera from the region. In Black Hawk Ranch time certain more hardy members of the East American Element were still present in the lowlands in a flood-plain habitat, and they presumably extended into the adjacent hills in cool canyons and on moister slopes. The occurrence of semiarid woodland and chaparral species on near-by upland slopes adjacent to the hardwood-deciduous flood-plain assemblage sug-

[1] Sediments of Black Hawk age in the area southeast of St. Mary's College, and about 7 miles west of the Black Hawk Ranch, contain reworked fossils derived from the Briones formation, which is now exposed on Las Trampas and Rocky ridges (K. A. Richey, oral communication, July 1939).

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gests that Black Hawk Ranch time was characterized by greater extremes of temperature and a somewhat lower rainfall than prevailed during the preceding Diablo and Neroly stages.

As was stated above, this trend toward increased continentality in the area seems related to rising topographic barriers at the west. The abundance of the East American Element in the Black Hawk Ranch flora is explainable on the basis of favorable local conditions, an explanation consistent with the restricted nature of the different plant communities in California during the Pliocene. It would appear that moderating oceanic conditions throughout the year provided suitable habitats in a region where the climate was rapidly becoming too dry for these relict types in lowland areas. Precipitation was in the neighborhood of 25 inches, and is thought to have been distributed biseasonally. Annual temperatures were more moderate than those now prevailing in the region, and summer temperatures in particular seem to have been lower.

Continued elevation of Las Trampas Ridge at the west following the Black Hawk Ranch stage is shown by the character of the sediments. There is evidence also of uplift in the Berkeley Hills by this time, for there are boulders of Moraga lava in the Tassajero conglomerates along the eastern front of the range. Elevation of these barriers at the west reduced moderating oceanic effects and resulted in a lower rainfall over the interior. As a result, semiarid species which had been limited to the drier uplands in Black Hawk Ranch time were able to invade lowland sites. Although mesic Miocene species disappeared from the lowland areas, they seem to have survived in their more humid upland habitats. This interpretation is suggested by their occurrence in a restricted upland habitat in Mulholland time, when the semiarid Oak woodland Component was dominant in the lowlands (chap. 5).

At the Mulholland locality, species of live oak (*Quercus*) are most abundant, and they formed a characteristic savanna about the immediate site of deposition. During this stage the stream banks were dominated by semiarid species of sycamore, cottonwood, and willow. Their associates in the semiarid depositional basin, where annual rainfall amounted to 15 or 17 inches, included members of the Southwest American Element now represented by equivalent species in southern California and southern Arizona. Oak woodland and chaparral communities covered the adjacent hills, and at higher elevations and on cooler slopes at lower altitudes, a border-redwood forest attained limited growth. Also living in this cooler region were *Acer bolanderi* Lesquereux, *Nyssa elaenoides* (Lesquereux) Condit, *Populus washoensis* Brown, *Quercus bockéei* Dorf, and *Quercus simulata* Knowlton. In contrast with their abundance in the Black Hawk Ranch assemblage, these form the rarest group at Mulholland. Although their relict persistence suggests that summer rains were disappearing, the presence of southern genera and species in the lowlands at Mulholland makes the assumption of summer precipitation at this time reasonable, for their nearest equivalents are now limited to areas with regular summer rains. In addition, there is evidence of the persistence of relict Miocene species into an even later stage (Sonoma) in coast-central California.

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Post-Mulholland floras are not known from the region directly east of San Francisco Bay, but they are represented 40 and 50 miles northward near Petaluma and Santa Rosa, as well as at the southern end of the Bay in the Santa Clara lake beds. These will now be considered because they have an important bearing on the later modifications of the northern and southern continental floras.

The Petaluma flora comes from two horizons in the area near Lakeville. The higher of these has been recorded as the Merced flora by Dorf (1930, p. 16), and is now considered to occur in the Upper Petaluma formation (chap. 7, pp. 186–187). The second locality is in the Lower Petaluma, 1½ miles to the north. The floras from both localities are essentially identical, but the Lower Petaluma is larger and thus contains species not represented in the Upper Petaluma. The flora is clearly of southern interior aspect, for it is dominated by members of the Oak woodland Component. Live oaks are predominant, and they formed a savanna-woodland over the region. Only one member of the flora, *Quercus orindensis,* has its nearest modern affinities in the southwestern United States. Larger collections here may be expected to reveal additional members of this southwestern group, for they persisted into Sonoma time in the region directly north. Like the Mulholland, the Petaluma has a subordinate Border-redwood Component, represented by species of *Arbutus, Ceanothus, Fraxinus,* and *Populus,* as well as a small-leafed derivative elm, *Ulmus moragensis.* The reduction in numbers of the East American and East Asian Elements in the Petaluma flora indicates its post-Mulholland age. This is also in agreement with the occurrence of *Neohipparion gidleyi* in the upper part of the Petaluma formation. Though larger collections must be obtained before a close age determination can be made for this flora, the 13 species in the Lower Petaluma suggest an age not older than Middle Pliocene. On this basis, the top of the Tolay volcanics, which are interbedded in the Lower Petaluma, would be of similar age. Whether the Pinole tuff had its origin in this region is a question which may well be raised here, for it is apparently contemporaneous (Wood *et al.,* 1941, table) and occurs in the region 25 miles southeast. Furthermore, volcanics similar in all respects to the Tolay have been recognized in the Potrero Hills (Morse and Bailey, 1935, p. 1441), an area directly north of the Pinole type section.

Following Petaluma time, temperatures became more moderate and there was an increase in rainfall. This is shown by the fact that the Sonoma flora, which occurs 20 miles north of Petaluma, is characterized by a dominant Redwood Component (chap. 7). It has a mesic coastal aspect, for it contains members of the North-coast coniferous Component whose nearest modern equivalents now find their southern limits of distribution on the humid coast of California 80 miles northwest of Santa Rosa. Also represented in the Sonoma flora are several relicts of the East Asian and East American Elements (*Castanea, Quercus, Trapa, Ulmus*), as well as members of the Southwest American Element now found in northern Mexico (*Ilex, Quercus*). The invasion of the cooler and moister Sonoma flora into this region previously occupied by the semiarid Petaluma flora seems to herald the beginning of the climatic trend that culminated in the Pleistocene. It may be noted that recent collections have shown

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the presence of *Populus washoensis* Brown in the lower part of the San Joaquin formation near Coalinga, which is considered to be of essentially Sonoma age, that is, early Upper Pliocene. These Miocene relicts represent survivors along the borders of marine embayments under moderating conditions, and it would appear that they also indicate summer precipitation at this later date. It is critical in this connection that members of the East Asian and East American Elements were eliminated first from the interior provinces (northern Great Basin, Columbia Plateau, central Great Basin) during the Lower Pliocene. Their earlier disappearance here seems explainable by decreased rainfall and higher evaporation, resulting in lowered precipitation at the interior as compared with the coastal area. Since the growing season for these plants coincides with the period of summer rainfall, it is to be expected that Miocene relicts would persist longer near the coast than in the interior.

The flora of the Santa Clara lake beds (Dorf, 1930, pp. 52–55) also represents a redwood forest, but it differs from the Sonoma in several important respects. Members of the East American and East Asian Elements, as well as those of the Southwest American Element now found in regions to the south, have not been recorded here, and there are no records of the North-coast coniferous Component. The Santa Clara contains a Sierra-Cascade Component which is not represented in the Sonoma near Santa Rosa. The fossil species making up this group have been compared with the following common members of the Sierra-Cascade forest extending from central Oregon southward into the north Coast Ranges and through the Sierra Nevada into the higher mountains of southern California. This forest also has a discontinuous distribution along the summits of the middle and south Coast Ranges.

Aesculus californica
Amelanchier alnifolia
Arbutus menziesii
Ceanothus integerrimus
Cercocarpus betuloides
Libocedrus decurrens
Pinus lambertiana
Prunus demissa
Ribes nevadense

The Santa Clara flora is cooler and more mesic in aspect than the vegetation in that region today, which represents a border-redwood forest with chaparral and oak woodland on near-by slopes. It is evident that there has been a trend toward lowered rainfall and higher summer temperatures in this region since Santa Clara time. This seems to have been due largely to the rising Santa Cruz Mountains to the west, which cast a rain shadow over the area, and form a barrier to the fogs that are of common occurrence on the windward slopes of the range. With the development of a drier climate on the leeward side of the mountains, and expansion of the semiarid oak savanna and chaparral communities, the redwood forest which had formerly extended out from the range was restricted 4 to 5 miles westward, within the mountains where precipitation is greater and evaporation lower than at the fossil locality. Members of the Sierra-Cascade Component, which had been associated with the redwood in the western United States during Miocene and Pliocene times, appear to have

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been segregated from that forest in the late Pliocene (Mason, 1936, p. 188). The Santa Clara flora is considered to be of late Upper Pliocene age, but it may possibly represent early Pleistocene time.

Nowhere in North America is the sequence of Pliocene floras now known to be so nearly complete as in the San Francisco Bay region. The salient features of floristic succession in this area may be summarized as follows:

1. Members of the East American and East Asian Elements dominate the Mio-Pliocene and early Lower Pliocene floras of west-central California. They form minor elements in early Middle Pliocene time, and persist as relicts in the coastal region into the early Upper Pliocene.

2. Relicts of the Caribbean Element are represented in the Mio-Pliocene Neroly flora, but are not certainly known from younger horizons except for *Persea*.

3. The Southwest American Element appears as a subordinate group by mid-Lower Pliocene time, and becomes dominant at the end of that stage and in the early Middle Pliocene. In the Upper Pliocene it assumes a subordinate role near the coast as the West American Element extends its range under the influence of a cooler and moister climate.

4. The first appearance of coast redwood in this region is in the Middle Pliocene Pinole tuff, where wood has been recorded at Hipparion Point (U. C. Mus. Paleont. 1037). A Sierra-Cascade Component was associated with the redwood forest during Middle and Upper Pliocene times. In the Upper Pliocene, members of the North-coast coniferous Component ranged south of the present southern limits of that forest. During the Pleistocene, members of the Closed-cone pine and Redwood Components also ranged southward along the coast (Chaney and Mason, 1930, 1933).

Central Sierra Nevada

Our knowledge of the later Tertiary floral sequence in the central Sierra Nevada is incomplete, for the floras that have been studied represent only Mio-Pliocene and Middle Pliocene stages. Nevertheless it is desirable to review them, because they illustrate the difference in aspect between the vegetation of this region and that of west-central California. Three of the five floras to be considered, the Remington Hill, Table Mountain, and Oakdale, are described in the present volume. The Mohawk flora from Plumas County, which was listed by Knowlton in his discussion of the floras of the auriferous gravels (1911), will be considered briefly on the basis of certain systematic revisions. One other, the Valley Springs flora, is reported here in preliminary manner for the first time. In the discussion which follows, these floras are considered in order of their age, starting with the oldest.

The oldest later Tertiary flora from the central part of the Sierra Nevada comes from the rhyolitic Valley Springs formation (Piper *et al.*, 1939), and, for reasons presented below, it is considered to be of late Upper Miocene age. The Valley Springs formation largely represents fluviatile materials derived from rhyolitic eruptions in the higher parts of the Sierra Nevada. These sediments

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were deposited unconformably on the Ione formation in the foothill region, and in some places rest on the pre-Cretaceous bedrock. The formation was laid down upon a surface characterized by moderate relief, except in the lowest foothill region, where it may have been nearly a plain.

In the Mokelumne area these sediments were carried along a channel south of the present Mokelumne River. It was in this channel, which descends from an elevation of 1500 feet on Mokelumne Hill to about 700 feet at Valley Springs 10 miles southwest, that the Valley Springs flora was laid down. The total number of species tentatively recognized includes the following 17 plants:[2]

Acer bolanderi Lesquereux
Acer cf. negundoides MacGinitie
Alnus merriami Dorf
Ceanothus sp. (cf. C. rigidus)
Ficus microphylla Lesquereux
Lyonothamnus mohavensis Axelrod
Mahonia hollicki (Dorf) Arnold
Persea pseudo-carolinensis Lesquereux
Pinus sp. (a fascicle of 2 needles)
Platanus dissecta Lesquereux
Quercus convexa Lesquereux
Quercus hannibali Dorf
Quercus simulata Knowlton
Salix californica Lesquereux
Sapindus oklahomensis Berry
Torreya sp. Mason
Umbellularia salicifolia (Lesquereux) Axelrod

The local distribution of the species at the three localities is as follows:

1. U. S. Geol. Survey loc. 6901. Chili Gulch, about ½ mile south of the town of Mokelumne Hill, at an elevation of about 1300 feet.

Acer bolanderi
Alnus merriami
Persea pseudo-carolinensis
Platanus dissecta
Quercus convexa
Quercus hannibali
Salix californica
Sapindus oklahomensis
Umbellularia salicifolia

2. U. S. Geol. Survey loc. 6903. From the old Menimae Tunnel of the Phoenix Mining Company. This is located near the Benson Brothers Mine, which is shown on the Economic Sheet of the Jackson Folio, about 5 miles south of the preceding locality and at essentially the same elevation.

Acer cf. negundoides
Ficus microphylla
Mahonia hollicki
Quercus convexa
Quercus simulata

3. U. S. Geol. Survey loc. 6904. The locality data read: "Rhyolite tuff of old shaft below Wheats, Jackson Folio." Rhyolite tuffs are exposed slightly more than 1 mile directly west of Wheats, at an elevation of 650 feet.

Ceanothus sp.
Ficus microphylla
Lyonothamnus mohavensis
Pinus sp.
Quercus hannibali
Quercus simulata
Salix californica
Torreya sp.

[2] The writer is particularly indebted to Dr. Roland W. Brown for permission to study this flora, which is now in the collections at the U. S. National Museum.

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The fossil localities are now at elevations ranging from 650 feet above sea level near Wheats to about 1300 feet at Chili Gulch and Menimae Tunnel 7 miles eastward, but the florules must have been laid down at a lower level, since uplift in the range has continued from Valley Springs time down to the present. The studies of Lindgren (1911), Matthes (1930), and Piper and his associates (1939) indicate that the Sierra Nevada had an initial western slope of approximately 90 to 100 feet per mile during Valley Springs time, and that this was increased during the later Cenozoic to its present average gradient of 180 feet per mile. This suggests that the Wheats locality had an elevation of not more than 300 feet during Valley Springs time, and that the florules from Chili Gulch and Menimae Tunnel were laid down about 500 to 600 feet above sea level.

Because the collections are small, it is not possible to base any conclusions on the relative abundance of the different species in the flora. It must be noted, however, that members of both the Arcto-Tertiary and the Madro-Tertiary Floras are represented, and that the semiarid Southwest American Element is sufficiently abundant to make up approximately 25 per cent of the flora. Members of the northern forest included such stream-bank species as *Acer bolanderi, Alnus merriami, Platanus dissecta,* and *Salix californica,* with *Mahonia hollicki, Pinus* sp., *Quercus simulata, Torreya* sp., and *Umbellularia salicifolia* occupying the adjacent valley bottoms and moister slopes. The drier sites supported such members of the Southwest American Element as *Quercus convexa, Q. hannibali,* and *Ceanothus* sp., with *Lyonothamnus mohavensis* and *Sapindus oklahomensis* occurring in the more open parts of the river valley. Predominantly of Arid Transition character and having a definitely Upper Sonoran aspect, the Valley Springs flora is believed to have lived under an annual rainfall of about 25 to 30 inches, distributed biseasonally.

There is a close relationship between the Valley Springs flora and the Table Mountain, located 23 miles southeast and laid down at an elevation of approximately 500 feet. Of the 17 Valley Springs species, 6 occur at Table Mountain. All the others might also be expected in that assemblage. Not only is a close relationship indicated in specific composition, but the members of the Arcto-Tertiary and Madro-Tertiary Floras seem to hold an essentially similar quantitative position in each flora, so far as can be judged from the limited Valley Springs collections. It is significant also that the climatic and life-zone relationships of the two floras are closely similar. Since the Table Mountain flora is considered to be of transitional Mio-Pliocene age, it follows that the Valley Springs cannot be much older; it is referred to the later part of Upper Miocene time.

It would thus appear that in this area no hiatus is represented between the periods of rhyolitic and andesitic eruption. In this connection it may be pointed out that Williams (1929) has shown that the Sutter formation at Marysville Buttes, which is considered to be of Mio-Pliocene age, is largely made up of rhyolitic tuffs which grade upward into andesitic materials. The formation is considered to be the detrital equivalent of the rhyolitic and andesitic deposits of the Sierra Nevada, admixed with sediments that are the equivalents in age

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of the gravels of the "intervolcanic period" of the Sierra Nevada. Attention has already been directed to a small flora from rhyolitic ash directly below the Neroly formation near Corral Hollow (p. 212). Louderback has pointed out that the andesitic part of the Neroly formation in this area probably was transported from the Sierra Nevada across the present Great Valley of California (1924, p. 17). It may be suggested that the rhyolites which occur below the andesites in the Valley Springs region had a similar origin. Because the floras from the rhyolites and lower andesites in both the Sierra Nevada and the inner Coast Ranges are essentially continuous from a floristic standpoint, it is concluded that no hiatus or "intervolcanic period" separates the Valley Springs and Mehrten formations. Significantly, in certain areas the Valley Springs grades upward into the Mehrten formation.

Three floras are now known from the lower part of the andesitic series in the central Sierra Nevada. The Remington Hill flora has been discussed in detail by Condit in chapter 2 of this volume. The following genera representing members of the Arcto-Tertiary Flora occur at this locality:

Acer	Crataegus	Smilax
Aesculus	Juglans	Ulmus
Berchemia	Liquidambar	Viburnum
Chamaecyparis	Sequoia	Vitis

This group formed a forest over the region and attained optimum development along the river valleys and on cooler slopes. Occurring in lesser numbers, and largely inhabiting drier and more exposed sites, were such members of the Southwest American Element as *Arctostaphylos martzi* Condit, *Ceanothus precuneatus* Axelrod, *Mahonia malheurensis* Arnold, *Platanus paucidentata* Dorf, *Populus prefremontii* Dorf, *Quercus douglasoides* Axelrod, and *Ungnadia clarki* Condit. The Remington Hill is considered to have lived under an annual rainfall of 35 to 40 inches and at an elevation in the vicinity of 2000 feet, during Neroly time.

The Mohawk flora is preserved in andesitic sediments which are reported to contain rhyolitic pebbles in their lower part. These beds were laid down at an elevation which may have been fully 1000 feet above the Remington Hill flora. An examination of the collections from this locality, which are now at the U. S. National Museum,[8] indicates that the Mohawk flora has a somewhat different aspect from that presented by Knowlton (1911):

Mohawk flora listed by Knowlton	*Present interpretation*
Juglans californica Lesquereux	Carya egregia (Lesquereux) LaMotte
Juglans egregia Lesquereux	Carya egregia (Lesquereux) LaMotte
Laurus californica Lesquereux	Persea pseudo-carolinensis Lesquereux
Magnolia lanceolata Lesquereux	Magnolia dayana Cockerell
Persea pseudo-carolinensis Lesquereux	Persea pseudo-carolinensis Lesquereux
Persea punctulata Lesquereux	Magnolia dayana Cockerell

[8] The writer is indebted to Dr. Roland W. Brown for the opportunity to examine the Mohawk flora and present this revised list.

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Mohawk flora listed by Knowlton	*Present interpretation*
Populus zaddachi Heer	Populus eotremuloides Knowlton
Quercus distincta Lesquereux	Quercus payettensis Knowlton
Quercus nevadensis Lesquereux	Quercus payettensis Knowlton
Rhus metopioides Lesquereux	Carya egregia (Lesquereux) LaMotte
Ulmus californica Lesquereux	Carya egregia (Lesquereux) LaMotte
Ulmus pseudo-fulva Lesquereux	Alnus sp.

In addition to these species listed by Knowlton, the following are also represented in the flora:

Arbutus matthesii Chaney
Berchemia multinervis (Al. Braun) Heer
Liquidambar pachyphyllum Knowlton
Pinus sp. (seed: cf. P. lambertiana)
Salix hesperia (Knowlton) Condit

Members of the semiarid Southwest American Element are absent from the comparatively large collections. This probably is to be attributed not to greater age as compared with the Remington Hill, but rather to the fact that the flora lived under an annual rainfall of 40 inches and more, and at an elevation above the upper altitudinal limits of semiarid woodland-chaparral vegetation on the windward slopes of the range. It is to be emphasized that in its present range the woodland-chaparral vegetation is also limited at higher elevations by increased precipitation and lower temperatures, and that a montane forest replaces it in such regions. On the basis of its composition and geologic occurrence, the Mohawk flora is assigned to the late Upper Miocene or basal Pliocene, and is considered to be essentially contemporaneous with the Remington Hill.

The Table Mountain flora, which is situated 90 miles south of Remington Hill and accumulated at an elevation about 1400 feet lower, likewise represents the vegetation of latest Miocene or earliest Pliocene time in the Sierra Nevada. Members of the Arcto-Tertiary Flora, which make up an important group in this flora, include such genera as:

Acer	Crataegus
Berchemia	Gleditschia
Carya	Platanus
Cercis	Rhododendron
Cornus	Ulmus

These plants are considered to have occupied the moister slopes and lowland valleys adjacent to the Table Mountain site of deposition. The drier and more exposed sites bordering these areas were inhabited by members of the Southwest American Element, including *Celtis kansana, Cercocarpus antiquus, Forestiera buchananensis, Mahonia prelanceolata, Quercus convexa, Q. dispersa,* and *Robinia californica.* Their comparatively large representation in the flora suggests that the trend to aridity in the lower foothill region since Valley Springs time had been sufficient for this element to have become diversified and well developed in more exposed sites bordering areas of deposition. It would ap-

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pear also that as a result of increased aridity the mesic elements had a more restricted occurrence than in Valley Springs time. Representing a change from the Arid Transition life-zone conditions of Valley Springs time, the Table Mountain flora is predominantly of Arid Transition–Upper Sonoran aspect. It lived under an annual rainfall of from 25 to 30 inches, which seems to have been distributed during both the summer and the winter months. During this stage, it may be assumed that vegetation at elevations below the Table Mountain locality was more xeric in aspect and that the mesic group had a subordinate role in the flora.

A transect of the central Sierra Nevada during late Miocene and early Pliocene time (Mohawk, Remington Hill, Table Mountain) reveals the following features with respect to climate and vegetation:

1. Rainfall increased from a minimum of 25 or 30 inches in the lower foothill area to more than 50 inches in the higher parts of the range, which at this time had elevations in the neighborhood of 3000 to 4000 feet (Matthes, 1930). At lower levels rainfall appears to have been of biseasonal occurrence, but at higher levels a more even distribution prevailed. In connection with this postulated type of rainfall distribution in the Sierra Nevada during late Miocene time, it is desirable to point out that comparable conditions occur at the present time in regions of biseasonal precipitation in the western United States. In the Rocky Mountains and in the southwestern United States, rainfall over the lowlands is distinctly biseasonal. With a rise in elevation, precipitation becomes heavier and the periods are less well defined, so that an even distribution is approached.

2. Summer temperatures were higher at lower levels than in the upper parts of the range, and presumably the evaporation rate in the foothill area was correspondingly higher.

3. In response to this climatic zonation, the vegetation shows gradual modification at successively higher levels. In the lower foothill area, floras are characterized by members of the Arcto-Tertiary Flora, but the Southwest American Element is sufficiently abundant to give the floras an Upper Sonoran aspect. With a rise in elevation into the more humid areas, members of the Oak woodland and Chaparral Components gradually become subordinate (Remington Hill) and finally disappear (Mohawk). A similar distribution still exists in the Sierra Nevada, for the digger pine woodland, of Sierra Madrean origin, which characterizes the foothill region is replaced at higher levels by the more mesic Sierra-Cascade forest of northern derivation.

There is a considerable stratigraphic break between these transitional Mio-Pliocene floras and the Oakdale stage, which is considered to represent Middle Pliocene time (see chapter 6). During this interval there was a marked change in the character of the vegetation in the lower foothill region of the Sierra Nevada. Such members of the Mio-Pliocene flora as *Persea pseudo-carolinensis* and *Platanus dissecta,* which are considered to have extended along stream banks through the lower foothill area and into the coastal regions, were com-

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pletely eliminated by Oakdale time. Also there is no record of members of the East American Element in the Oakdale stage. If they survived in the central Sierra Nevada during Oakdale time, they must have been limited to higher elevations where rainfall was greater and temperatures were more moderate. No typical members of the northern forest whose nearest living descendants now form part of the Transition forest in the Sierra Nevada are represented in the Oakdale flora, although they were present earlier in the Pliocene. These likewise must have been limited to higher elevations, since the Oakdale region had an annual rainfall of from 18 to 20 inches. It has been noted that by Valley Springs time the Southwest American Element was becoming an important floristic group on the lower flanks of the central Sierra Nevada. By Table Mountain time a larger number of species can be referred to this element, and they hold a more important place in the flora from a quantitative standpoint than during the preceding Valley Springs stage. In response to the increased aridity over the lower flanks of the range, members of the mesic northern forest were largely eliminated by Oakdale time, when members of the Southwest American Element were predominant. An oak savanna-woodland characterized the interfluvial areas, and its associates included such shrubs as *Arctostaphylos, Ceanothus, Photinia,* and *Ribes.* Stream banks in the Oakdale area were inhabited by *Celtis, Populus, Robinia, Salix,* and *Sapindus.*

Since the sequence of Pliocene floras in the central Sierran area is relatively incomplete, the floristic modifications here are less well known than in the San Francisco Bay region. It is difficult to compare the successions of floras in these two provinces because the coastal floras were deposited within a few hundred feet of sea level, whereas those in the central Sierra Nevada were laid down at elevations ranging from 200 to over 2000 feet above sea level. For this reason, only the floras from the lower Sierran slopes (Valley Springs, Table Mountain, Oakdale) can be compared directly with those of the coastal region. The most important differences to be noted in the floristic sequence in the two provinces may be listed as follows:

1. Whereas the Southwest American Element forms an important group in the lower Sierran foothills in the late Miocene, it is practically absent from the San Francisco Bay region at this time. Dominating the lower slopes of the central Sierra Nevada in the early Lower Pliocene, it does not become conspicuous in the coastal region until the middle of that stage, and does not dominate until late Lower or early Middle Pliocene time.

2. The East Asian and East American Elements have a moderate representation in the foothills of the central Sierra Nevada in the latest Miocene, but they dominate during this stage in the cooler coastal area. Although they apparently had disappeared from the lower central Sierran foothill region by the Middle Pliocene, members of these elements survived into Upper Pliocene time in the coastal region.

3. The mesic coast redwood and its humid associates were eliminated from the middle foothill region of the central Sierra Nevada by the early Pliocene,

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but their equivalents have survived down to the present in the cooler coastal region.

Summary

These studies of the later Tertiary floras of central California emphasize the complexity of Pliocene vegetation. This is fully to be expected during such an epoch as the Pliocene, when topographic diversity and micro-climates controlled the distribution of vegetation.

Floral succession in the western United States during later Tertiary time largely involved a coastward and northward movement of semiarid woodland and chaparral vegetation, which gradually replaced mesic forests of northern derivation at low to moderate elevations. Thus it is understandable that the stage during which certain elements appear and others are eliminated will vary in the several provinces, depending on position with respect to latitude, elevation, mountain ranges, and the ocean. Specific relationship between Pliocene floras of different provinces may therefore be an indication not of contemporaneity, but of different age. Only by establishing a relatively complete floristic sequence for each province will it be possible to correlate more closely the diverse floras of the coastal and interior areas of deposition.

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9

The Alvord Creek Flora

DANIEL I. AXELROD

Introduction

Fossil plants were collected first from the Alvord Creek formation[1] of southeastern Oregon by Fuller during his geological study of the Steens Mountain area (1931). In a preliminary report on this material Chaney identified 11 species, and 9 of these were considered to be present in the Mascall flora (*in* Fuller, 1931, p. 51). A second and larger collection was made at Alvord Creek by MacGinitie in connection with his investigation of the Trout Creek flora, 30 miles southeast (1933). Both these collections have been incorporated with additional material obtained by the writer with the assistance of James F. Ashley during the summer of 1939, and form the basis of the present report.

The Alvord Creek occupies an important place among the late Tertiary floras of the western interior. Previous to the publication of this volume, the Pliocene record of the northern Great Basin has been represented by only 2 species in the Alturas flora, of northeastern California (Dorf, 1930, pp. 51–52). The Alvord Creek flora contains 26 species and is of Lower Pliocene age. Its occurrence in proximity to the Miocene Trout Creek (MacGinitie, 1933), Upper Cedarville (LaMotte, 1936), and Succor Creek (Brooks, 1935; Smith, 1939*b*) floras is critical, since it adds important data regarding post-Miocene climatic and floral changes in the northern Great Basin. The Alvord Creek also occupies a geographically intermediate position between the Pliocene floras of the Columbia Plateau (Deschutes, Dalles, Troutdale, Ellensburg) and those of the central Great Basin (Upper Truckee, Esmeralda). For this reason it materially supplements our understanding of Pliocene plant geography to the lee of the Sierra-Cascade barrier, and provides a basis for north-south correlation in this region.

Geologic Occurrence

Steens Mountain is the outstanding topographic feature of the Alvord Creek area. This fault-block range extends north-south for over 60 miles and attains an elevation of nearly 10,000 feet in its central part. The Alvord Creek fossil plant localities are situated near the eastern base of the high central part of the range directly west of Alvord Ranch, at an altitude of 4500 feet.

The high eastern scarp of central Steens Mountain presents the most extensive rock exposures in southeastern Oregon. The following section represent-

[1] Following the rules of geological nomenclature (Bull. Geol. Soc. Amer., vol. 44, pp. 433–435, 1933), the *Alvord Creek beds* described by Fuller are here designated the *Alvord Creek formation.*

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ing the major formations on the scarp is not exposed completely in any one area, but outcrops are almost continuous for more than 5000 feet on the scarp:

Crest of range	*Approx. maximum thickness in feet*
Steens basalt	3000
Steens Mountain andesite	1500
Pipe Creek volcanics	1500
Alvord Creek formation	950
Total	6950

The Alvord Creek formation (see plate 40) consists for the most part of bedded tuffs which occur in several widely separated areas along the lower flanks of the range west of Alvord Ranch. It has not been possible to correlate these isolated exposures certainly, owing to their variable lithology, but Fuller has pointed out that they probably belong to the same formation. Although the beds are roughly horizontal, they have been deformed locally by later intrusions which have also baked and altered the sediments. Impressions of leaves, seeds, and cone scales have been collected at two major localities in the middle of the formation.

Locality 601N, University of California paleobotanical series, is on the main scarp a few hundred yards north of the valley of Alvord Creek. Here the formation has a southerly dip of about 7° and a maximum thickness of about 950 feet. The following section is exposed (Fuller, 1931, pp. 47–48):

	Maximum thickness in feet
White tuff	100
Flow of basic andesite	100
Light tuffaceous sediments containing horizons of opalized shale rich in fossil leaves	200
Buff stratified tuff	50
Brownish, altered trachytic tuffs	500
Total	950

Lenses of agglomerate and conglomerate occur locally, but in general they are infrequent.

Locality 601 is at an old prospect on the east-facing slope of the south fork of Alvord Creek within 100 yards of the point where it swings westward into the main part of the range; this is about ½ mile south of locality 601N. The formation is roughly horizontal in this area, and has a thickness of nearly 500 feet (Fuller, 1931, p. 48). The lowest strata apparently correspond to the basal member listed above, but only about 50 feet are exposed. Higher in the section the well bedded tuffs are light-colored. In the upper part of this zone, and about 30 feet below a cliff formed by a prominent basaltic dike, a shale horizon some 3 to 4 feet thick is rich in fossil plants.

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The brownish, opalized plant-bearing shales are finely bedded and some of them have a thickness of ⅛ inch or less. Such deposits are commonly interpreted as lacustrine in origin. The position of the leaves, which is always flat and parallel to the bedding plane, confirms the indication of deposition in standing water. Their occasional matted condition suggests accumulation in relatively quiet water where wave and wind action were at a minimum. It would appear also that most of the leaves were shed by plants living near at hand, for the majority are complete and well preserved.

Composition and Physical Indications

The Alvord Creek flora is represented by 26 species, among which there are 8 conifers, 1 monocotyledon, and 17 dicotyledons. Nearly all of these are represented by identical or closely related species in previously described Miocene and Pliocene floras in the western United States.

Systematic List of Species

Spermatophyta
- Gymnospermae
  - Coniferales
    - Pinaceae
      - Abies alvordensis new species
      - Abies klamathensis new name
      - Picea lahontense MacGinitie
      - Picea sonomensis Axelrod
      - Pinus alvordensis new species
      - Pinus sp.
      - Pseudotsuga sonomensis Dorf
    - Cupressaceae
      - Juniperus alvordensis new species
- Angiospermae
  - Monocotyledones
    - Naiadales
      - Potamogetonaceae
        - Potamogeton sp.
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Populus payettensis (Knowlton) new combination
        - Populus pliotremuloides Axelrod
        - Salix payettensis new species
    - Fagales
      - Betulaceae
        - Carpinus grandis Unger
    - Ranales
      - Berberidaceae
        - Mahonia reticulata (MacGinitie) Brown

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Rosales
  Rosaceae
    Amelanchier alvordensis new species
    Cercocarpus antiquus Lesquereux
    Cercocarpus holmesii (Lesquereux) new combination
    Photinia sonomensis Axelrod
    Prunus harneyensis new species
    Rosa alvordensis new species
    Sorbus harneyensis new species
  Leguminosae
    Amorpha condoni Chaney
Sapindales
  Anacardiaceae
    Rhus alvordensis new species
  Aceraceae
    Acer alvordensis new species
Rhamnales
  Rhamnaceae
    Ceanothus precuneatus Axelrod
Ericales
  Ericaceae
    Arbutus idahoensis (Knowlton) Brown

The largest families are the Rosaceae, with 7 species representing 6 genera, and the Pinaceae, with 7 species distributed in 4 genera. *Amelanchier alvordensis, Cercocarpus antiquus,* and *Acer alvordensis* are the most abundant species, followed by *Rhus alvordensis.* Together they make up nearly 90 per cent of the flora, which is represented by approximately 500 specimens. None of the remaining species is common, most being represented by not more than 3 or 4 specimens.

One of the notable features of the Alvord Creek flora is that oaks have not been encountered in the collections. This has been difficult to explain, since they are common in near-by Miocene floras and might be expected to have survived into Alvord Creek time. Furthermore, as will be pointed out on a later page, oaks form an important part of the vegetation in all areas where the fossil flora shows relationship to living plant communities.

In order to interpret the physical conditions of Alvord Creek time, the fossil flora will be compared first with modern vegetation which resembles it most closely. The Alvord Creek species may be grouped into four elements, as listed in table 21. Obviously such a division cannot be rigid, for some fossil species are related equally to plants found in more than one modern group. Nevertheless, most of the fossil species typify the elements to which they have been assigned, and provide evidence of value in reconstructing the Alvord Creek forest and its environment.

Living representatives of three components listed in table 21, the Sierra-

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TABLE 21

ELEMENTS AND COMPONENTS OF THE ALVORD CREEK FLORA

Fossil species	*Equivalent living species*
West American Element	
Sierra-Cascade Component	
Abies klamathensis	A. shastensis Lemmon
Acer alvordensis	A. macrophyllum Pursh
*Amelanchier alvordensis	A. alnifolia Nuttall
*Amorpha condoni	A. californica Nuttall
*Mahonia reticulata	M. repens (Lindley) Don
*Picea sonomensis	P. breweriana Watson
*Pinus alvordensis	P. contorta Douglas
*Pinus sp.	P. ponderosa Douglas
*Populus pliotremuloides	P. tremuloides Michaux
*Pseudotsuga sonomensis	P. taxifolia (Lambert) Britton
*Rosa alvordensis	R. pisocarpa Gray; spp.
*Salix payettensis	S. fluviatilis Nuttall (group)
*Sorbus harneyensis	S. californica Greene
Rocky Mountain Component	
*Amelanchier alvordensis	A. alnifolia Nuttall
*Amorpha condoni	A. californica Nuttall
*Mahonia reticulata	M. repens (Lindley) Don
Picea lahontense	P. engelmannii Engelmann
*Pinus alvordensis	P. contorta Douglas
*Pinus sp.	P. ponderosa Douglas
Populus payettensis	P. angustifolia James
*Populus pliotremuloides	P. tremuloides Michaux
*Prunus harneyensis	P. virens Standley
*Pseudotsuga sonomensis	P. taxifolia (Lambert) Britton
*Rhus alvordensis	R. glabra Linnaeus
*Rosa alvordensis	R. macounii Greene
*Salix payettensis	S. fluviatilis Nuttall (group)
*Sorbus harneyensis	S. scopulina Greene
Southwest American Element	
Chaparral Component	
Ceanothus precuneatus	C. cuneatus Nuttall
Cercocarpus antiquus	C. betuloides Nuttall
Cercocarpus holmesii	C. paucidentatus (Watson) Britton
Photinia sonomensis	P. arbutifolia Lindley
Conifer woodland Component	
Arbutus idahoensis	A. arizonica Sargent
Juniperus alvordensis	J. scopulorum Sargent
East American Element	
*Carpinus grandis	C. caroliniana Walter
*Prunus harneyensis	P. serotina Ehrhart
*Rhus alvordensis	R. glabra Linnaeus
East Asian Element	
Abies alvordensis	A. recurvata Masters
*Carpinus grandis	C. laxiflora Blume
*Picea sonomensis	P. asperata Masters; spp.

*Species occurring in more than one component.

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Cascade, Rocky Mountain, and Chaparral, live in close proximity in the Klamath Mountain area of northern California, 200 miles southwest of Alvord Creek. In this region there are 17 modern equivalents of the 25 woody plants of the fossil flora. Besides containing a large number of Alvord Creek living equivalents, the Klamath Mountain region is suggestive of the physical conditions during Alvord Creek time because all the Pliocene dominants are represented here by related species. In addition, this is the only region where the relatively xeric shrubs *Ceanothus, Cercocarpus,* and *Photinia* live in proximity to such endemics as *Abies shastensis* and *Picea breweriana,* and to such typically high-montane species as *Picea engelmannii, Pinus contorta, Populus tremuloides,* and *Sorbus californica.*

Two broad floristic areas characterize the Klamath Mountain area, and correspond roughly to the windward and leeward slopes. A third region, and one of high endemism, is found in the summit part of this mountainous country. A redwood forest dominated by *Sequoia sempervirens* occupies the humid coastal valleys along windward slopes, and certain equivalent Alvord Creek species, such as *Acer macrophyllum, Amelanchier alnifolia, Pseudotsuga taxifolia,* and *Rosa pisocarpa,* range into this area. For the most part the fossil species have leaves of smaller size and thicker texture than their modern representatives in this mesic coastal province. For example, *Acer alvordensis* has leaves which are small and often lobed to the base of the blade. These can be matched only by leaves found on *macrophyllum* growing in semiarid interior regions. Likewise, *Amelanchier alvordensis* is represented in the modern flora by leaves of the serviceberry as found in interior rather than in humid coastal areas. Because the dominant Alvord Creek species reflect conditions never found in the coastal region—limited rainfall, high ranges of temperature, and ample sunshine—it is evident that the Alvord Creek is not ecologically correlated with the vegetation on the windward slopes of the Klamath Mountain area. This is suggested also by the absence at Alvord Creek of *Sequoia langsdorfii,* the fossil equivalent of *S. sempervirens,* as well as of fossil representatives of such regular redwood associates as *Abies grandis, Acer circinatum, Alnus rubra, Chamaecyparis lawsoniana, Rhamnus purshiana, Rhododendron californicum, Thuja plicata,* and *Tsuga heterophylla.*

The humid forest extends inland from the coast for some distance, but is replaced rapidly by an Arid Transition forest at the interior. This area is one of rugged topography and sharp climatic contrasts over short distances. As a result, the semiarid digger pine forest (*Pinus sabiniana* Douglas) and chaparral associations extend into the region from the borders of Sacramento Valley and overlap the Transition forest which grows at higher elevations and on cooler slopes (see pl. 41, fig. 2). This forest is characterized by the Sierra-Cascade association (Clements, 1920) and the *Arbutus-Quercus* association of the broad-sclerophyll climax (Cooper, 1922). The latter is the more xeric of the two, but they are closely associated. The following species in these Arid Transition communities have equivalents in the Alvord Creek flora:

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Acer macrophyllum	Pinus ponderosa
Amelanchier alnifolia	Pseudotsuga taxifolia
Amorpha californica	Rosa pisocarpa
Mahonia repens	

It is significant that the serviceberry and maple in this forest have leaves which closely resemble Alvord Creek species in size, texture, and lobation. Such plants as *Arbutus menziesii, Quercus kelloggii, Q. chrysolepis,* and *Q. garryana* give this region a distinctive physiognomy, but only the madrone is represented generically in the Alvord Creek flora. Fossil equivalents of the oaks might be expected at Alvord Creek, for they occur in the Miocene floras of the adjacent region together with correlatives of the above-listed species.

As was noted above, the drier slopes bordering the broad-sclerophyll and Sierra-Cascade forests in this region support chaparral. Three equivalent Alvord Creek species, *Ceanothus cuneatus, Cercocarpus betuloides,* and *Photinia arbutifolia,* are represented in this community, and often are scattered through the open parts of the forest. *Juniperus californica* also lives here, and may be considered an equivalent of the Alvord Creek juniper, although the latter seems more nearly related to *J. scopulorum* of the Rocky Mountains.

With rising elevation, the Sierra-Cascade forest and its associated broad-sclerophyll and chaparral communities give way in the Klamath Mountain region to a high-montane forest (see pl. 41, fig. 1). Along the crest of South Fork Mountain and Trinity Summit live *Abies shastensis, Picea breweriana, Pinus contorta, Populus tremuloides,* and *Sorbus sitchensis,* all with related species in the fossil flora. The presence of Canadian life-zone conditions here does not necessarily mean that they existed in the Alvord Creek area at the time of floral deposition. These plants regularly descend to lower levels in favorable topographic areas and may be found in the Sierra-Cascade forest in California and Nevada. *Sorbus* is found as low as 5000 feet in the Sierra Nevada, and MacGinitie reports it on South Fork Mountain with *Abies shastensis, Acer macrophyllum, Amelanchier alnifolia, Pinus ponderosa, Pseudotsuga taxifolia,* and *Rosa pisocarpa* (oral communication, July 1940), all with equivalents in the fossil flora. The lodgepole pine, *Pinus contorta,* has a similar distribution on the north coast of California adjacent to the redwood and north-coast coniferous forests. The Shasta fir, *Abies shastensis,* ranges from Mount Hull and Snow Mountain in Lake and Glenn counties northward through the Klamath Mountains and occurs commonly in the Sierra-Cascade forest at the north. *Picea breweriana,* the closest American equivalent of *P. sonomensis,* lives at elevations above 6000 feet in northwestern California. Sudworth, however, reports it as low as 4500 feet in the Trinity Mountains above Dedrick, and he states also that it has been reported from the lower slopes of Mount Shasta near Black Butte (1908, p. 86), which is now in the lower part of the Sierra-Cascade forest.[2]

[2] Intensive logging and fire presumably have destroyed this relict colony. It cannot be doubted that many other species had comparable outpost occurrences which have disappeared within the past century.

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The fossil equivalent, *P. sonomensis,* is represented in the Alvord Creek flora by only a few seeds, which may well have been transported to the site of deposition from a more distant area. It seems likely that the equivalents of such species as *Picea engelmannii, Populus tremuloides, Pinus contorta,* and *Sorbus californica* also lived in areas removed from the immediate Alvord Creek site of deposition, for they form an even rarer element in the flora, as judged from their scarcity as fossils.

Many equivalent Alvord Creek species in the Klamath Mountain region have a wide distribution in the western United States. A number of their fossil equivalents form an important part of the Rocky Mountain Component of the West American Element, as listed in table 21. Only 3 of these 14 species are not represented in the Klamath Mountain area by the same or by a closely similar plant. *Prunus virens* is a western segregate of *P. serotina* of the East American Element, and is not known from the Pacific region. *Rhus glabra* is not represented in California, but it occurs in northeastern Oregon 200 miles north of Alvord Creek. *Populus angustifolia* is unknown in the Klamath Mountain area, but *P. trichocarpa* probably represents it ecologically. The relationships between these cottonwoods are not so close, however, as those between the species of *Sorbus* and *Rosa* in the two areas. Nevertheless, it must be noted that *P. angustifolia* has a relict occurrence in western Nevada and southern California with the Sierra-Cascade forest. This is significant from a historical standpoint, for *P. payettensis,* the fossil equivalent of *P. angustifolia,* occurs with members of the Sierra-Cascade and Rocky Mountain Components, as well as with the Redwood and North-coast coniferous, in northern Great Basin Miocene floras. Close resemblances between the Rocky Mountain and Sierra-Cascade Components are fully to be expected in view of their later Tertiary history (Axelrod, 1940*b,* pp. 482–483).

The Transition forest in the southern Rocky Mountains is bordered regularly at lower levels by living equivalents of the Conifer woodland and Chaparral Components of the Southwest American Element. Five species representing these components, *Arbutus arizonica, Ceanothus cuneatus, Cercocarpus betuloides, C. paucidentatus,* and *Juniperus scopulorum,* have equivalents in the Alvord Creek flora. In this region of diverse relief they intermingle in much the same manner as is described above for representatives of the Sierra-Cascade, Chaparral, and Conifer woodland Components in California. Three species in the southern Rocky Mountains, *Arbutus arizonica, Cercocarpus paucidentatus,* and *Juniperus scopulorum,* are not known in California, but all of them are represented there generically. *Photinia* forms an important part of the chaparral in California, but is unknown in this community elsewhere in the western United States. The woodland and chaparral of the southern Rocky Mountains and adjacent region are related genetically to those in California. Since both were differentiated from the more generalized Madro-Tertiary Flora in late Tertiary time (Axelrod, 1940*b,* pp. 482–483), it is natural that there should still be a close resemblance between them.

The components just discussed, the Sierra-Cascade and Rocky Mountain of

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the West American Element and the Conifer woodland and Chaparral of the Southwest American Element, contain 23 of the 25 woody plants in the Alvord Creek flora. When the distribution of the living equivalent species is considered according to life zones, as shown in table 22, certain additional facts appear which have an important bearing on an interpretation of the Alvord Creek flora; also included in this table are data for the East Asian and East American Elements. All 23 species now living in the western United States occur in the Arid Transition zone, and 16 of these range also into the Upper Sonoran. Five of the 23 are found in the Humid Transition, and 5 others, which are

TABLE 22

LIFE-ZONE INDICATIONS OF LIVING EQUIVALENT ALVORD CREEK SPECIES

West American species (Total, 23)	*Upper Sonoran*	*Transition*		*Canadian*
		Arid	*Humid*	
Abies shastensis	..	x	x	x
Acer macrophyllum	x	x	x	..
Amelanchier alnifolia	x	x	x	..
Amorpha californica	x	x	..	..
Arbutus arizonica	x	x	..	x
Ceanothus cuneatus	x	x	..	..
Cercocarpus betuloides	x	x	o*	..
Cercocarpus paucidentatus	x	x	..	..
Juniperus scopulorum	x	x	..	..
Mahonia repens	x	x	..	..
Photinia arbutifolia	x	x	..	..
Picea breweriana	..	x	..	x
Picea engelmannii	..	x	o	x
Pinus contorta	..	x	o	x
Pinus ponderosa	..	x	o	..
Populus angustifolia	x	x	..	..
Populus tremuloides	x	x	o	x
Prunus virens	x	x	..	..
Pseudotsuga taxifolia	..	x	x	..
Rhus glabra	x	x	..	..
Rosa spp.	x	x	x	..
Salix fluviatilis	x	x	..	..
Sorbus californica	..	x	..	x
Total	16	23	10	7

East American and East Asian species (Total, 4)	*Carolinian*	*Alleghenian*	*Canadian*
Abies recurvata	..	x	x
Carpinus caroliniana	x	x	..
Picea asperata, wilsoni, etc.	..	x	x
Prunus serotina	x	x	..
Total	2	4	2

*Species marked by an o in the Humid Transition zone range only to the borders of that zone.

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marked by a letter o, may be found on the borders of that zone. It must be noted, however, that all of them range also into the Arid Transition. The same relation holds for the 7 species that range upward into the Canadian zone. This purely numerical consideration of the life-zone aspects of the flora suggests that the Alvord Creek was predominantly an Arid Transition assemblage, and that it lived in a region bordering Upper Sonoran rather than Humid Transition conditions. This interpretation agrees with the character of the plants in the flora, as well as with the relative abundance of the different ecological groups.

It has already been pointed out that such Alvord Creek dominants as *Acer alvordensis* and *Amelanchier alvordensis* are represented by leaves which resemble those produced by modern species in the semiarid and interior rather than in the humid and coastal parts of their distribution. On this basis the Alvord Creek flora must have been more nearly Upper Sonoran than Humid Transition in aspect. The presence of typical Upper Sonoran plants in the flora supports this interpretation. Judging from the occurrence of their living equivalents, the fossil species of *Ceanothus, Cercocarpus,* and *Photinia* form a narrowly restricted ecologic group whose comparative abundance at Alvord Creek indicates that relatively semiarid conditions must have existed near the Alvord Creek site of deposition. It is therefore understandable that *Acer alvordensis, Cercocarpus antiquus,* and *Amelanchier alvordensis* should dominate the flora. Their nearest living relatives form communities along stream banks sufficiently dense so that they would be expected to contribute a preponderance of leaves to accumulating sediments in areas of limited rainfall. The only plants in the flora that can be considered as approaching Humid Transition conditions are such members of the East American and East Asian Elements as *Carpinus grandis* and *Prunus harneyensis.* Their poor numerical representation, however, suggests that they had only a limited development in the region, and that they occurred probably on cooler slopes away from immediate sites of deposition. This interpretation is consistent with the fact that all specimens representing these species show signs of transport from more distant areas. If the Alvord Creek flora had lived in a region bordering Humid Transition conditions, these species would be expected to have a greater representation in the flora. Likewise, members of the montane forest would be more abundant, and the species of *Acer, Amelanchier, Arbutus,* and *Populus* would be represented by leaves similar to those produced by their modern equivalents in the more humid parts of their ranges. Finally, the Upper Sonoran species of *Ceanothus, Cercocarpus,* and *Photinia* would form a less prominent element in the flora. It may be concluded that the Alvord Creek flora, which is predominantly of Arid Transition aspect, lived in a region bordering Upper Sonoran rather than Humid Transition conditions.

There is a small group of plants in the Alvord Creek flora whose nearest relatives no longer live in the western United States. As is shown in table 21, two equivalent species, *Carpinus caroliniana* and *Prunus serotina,* live in the eastern United States. These members of the East American Element make up an important part of the forests in the eastern United States, but their fossil

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representatives are subordinate at Alvord Creek. Another equivalent Alvord Creek species, *Rhus glabra,* attains best development in the eastern United States, but ranges westward through the Rocky Mountains and into northeastern Oregon, where it occurs on the Deschutes River 150 miles north of Alvord Creek. Other typically eastern species which are represented by somewhat similar plants in the western United States, and have equivalents in the Alvord Creek flora, include the following:

Alvord Creek species	*Related species in eastern North America*
Amelanchier alvordensis	A. alnifolia
Amorpha condoni	A. fruticosa
Juniperus alvordensis	J. virginiana
Populus pliotremuloides	P. tremuloides
Salix payettensis	S. fluviatilis

In the case of *Juniperus,* the western species is essentially a geographic segregate of a phylad extending across the continent. The willow and aspen are widely distributed in North America and have no close floral significance. *Amorpha fruticosa* has leaflets that may at times be indistinguishable from those of *A. californica,* which has been considered as more probably related to *A. condoni.* Aside from the plants listed above, such Alvord Creek genera as *Picea, Pinus, Rosa,* and *Sorbus* occur also in eastern North America, but their species there seem more remotely related to the Alvord Creek fossils than the western species discussed above. Nevertheless, the common holarctic derivation of these genera is indicated by the fossil record, and they may therefore be expected to show some relationship to the Alvord Creek flora, the bulk of which had an origin in the Arcto-Tertiary Flora.

In addition to the small East American Element, the Alvord Creek flora also has a few members of the East Asian Element. One of the conifers, *Abies alvordensis,* most nearly resembles *A. recurvata* of China and Japan. Another conifer, *Picea sonomensis,* shows relationship to such Asiatic species as *P. asperata, P. likiangensis, P. wilsoni,* and others, as well as to the American *P. breweriana.* Significantly, the Alvord Creek *Carpinus* is represented also in eastern Asia by a closely similar species, *C. laxiflora* Blume, which is not readily separable from *C. caroliniana.* As in the case of the East American Element, a number of other Alvord Creek genera are represented also in eastern Asia. Their species, however, do not seem so closely related to the Alvord Creek fossils as the western plants already discussed. The following Alvord Creek genera are found in China and Japan:

Abies	Photinia	Pseudotsuga
Acer	Picea	Rhus
Amelanchier	Pinus	Rosa
Carpinus	Populus	Salix
Juniperus	Prunus	Sorbus
Mahonia		

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All these except *Photinia* and *Pseudotsuga* occur also in eastern North America, and there are certain species in most of these genera that are essentially identical in the two areas. There is a strong relationship between the modern forests of eastern Asia and eastern North America, and the Miocene forest of western North America forms an important link between them.

Summarizing the relationships of the Alvord Creek flora to modern vegetation: it is evident that the flora most nearly resembles modern vegetation in the inner Klamath Mountain region of northern California. Here Arid Transition and Upper Sonoran associations overlap in a region of diverse relief and climate, and typically high-montane species descend into this zone in favorable micro-climatic areas. Of the 25 woody plants in the flora, 17 have their nearest equivalents in this region, and all the dominants are here. Relationship is shown also by modern vegetation in the southern Rocky Mountains, where there are 5 species representing the Rocky Mountain, Conifer woodland, and Chaparral Components that are not found in northern California. Two species have equivalent representatives in eastern North America and 2 others are found in eastern Asia, but 1 in each of these has a similar species in western North America.

Vegetation showing relationship to the fossil flora is distributed through a vertical range of some 3000 feet. Nevertheless, there are reasons for assuming that relief of similar magnitude may not have been present in the Alvord Creek region at the time of floral deposition.

Geological evidence suggests that the flora was laid down in a lake basin surrounded by a region of moderate topographic diversity. Volcanic activity was prevalent in the region during Alvord Creek time, and since cones of the explosive type are indicated, volcanoes of some height may have been present. There probably were no high cones in the immediate vicinity of the plant locality, for the greater part of the formation consists of medium to fine-grained deposits. The rarity of agglomerates and breccias in the deposits also supports this interpretation. Coarse deposits probably would have been transported into the basin in greater abundance if a highland region had lain near at hand, for the climate was semiarid at this time. Thus it seems probable that the Alvord Creek volcanics were derived largely from cones located at some distance from the immediate site of deposition.

The past and present distribution of vegetation related to the Alvord Creek flora supports this interpretation that the basin of deposition may have been in a region of moderate relief. It has been pointed out that modern vegetation in the western United States related to the fossil flora often has a wide vertical distribution, depending on the topographic nature of the country, and on the presence of compensatory sites in the zones above and below those of normal species occurrence. In an ecotone between the upper and lower associations it seems clear that there would be an overlapping of otherwise widely separated vegetations. It is significant that an ecotone of this type may exist in areas of relatively low relief where the climate is subhumid. Such an environment may be seen today over a wide area on the plateau north of Mount Lassen. In this

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region there is a complete intermingling of Sierra-Cascade, woodland, and chaparral associations, and typically upland species descend into this Arid Transition region along cold streams from higher levels 10 or more miles distant. All these communities are now contributing their leaves and seeds to medium- and fine-grained deposits such as occur commonly in middle and later Tertiary basins of deposition over a wide area in the western United States.

A closely similar ecotone is believed to have occurred between montane and woodland-chaparral vegetation in the northern Great Basin in late Tertiary time. It is this overlap between two widely different types of vegetation which provides another basis for considering that the occurrence of representatives of diverse modern vegetation zones in a fossil flora need not always indicate the presence of a highland region immediately bordering the basin of deposition. It is fully understood, of course, that when plant remains are fragmentary and battered they may be interpreted as having been carried into the site of accumulation from more distant areas (Chaney and Mason, 1933, p. 74). The present discussion, however, is concerned with the occurrence of well preserved plant remains representing diverse units of modern vegetation which apparently lived at no great distance from the sites of deposition. The salient features of the later Tertiary ecotone accounting for such occurrences may be summarized as follows:

1. There is evidence that equivalents of the modern redwood, north-coast coniferous, Sierra-Cascade, and Rocky Mountain forests made up an integral part of the generalized Miocene forest. Equivalents of high-montane endemics also appear to have formed an important part of this forest, which had a wide distribution over the western interior when conditions were milder than those of today. As this mesic forest was restricted coastward and upward into mountainous areas in response to increased aridity at the interior in the later Miocene, the Madro-Tertiary Flora, of generalized composition, migrated northward and overlapped the retreating forest, which persisted in favorable sites over lowland and moderately upland areas. It is this overlap that accounts for the proximity of woodland and chaparral to equivalents of high-montane endemics.

2. Late Cenozoic segregation of the generalized Arcto-Tertiary and Madro-Tertiary Floras in response to climatic changes has resulted in the differentiation of the modern derivative associations of the montane and woodland climaxes which now have distinct climatic and geographic ranges in the western United States (Axelrod, 1940*b*, pp. 482–484).

3. Since the wide distribution of the relatives of certain montane endemics brought them into contact with diverse types of climate and vegetation, it has been suggested that the concept of ecospecies may also have an important place in interpreting some of these occurrences (Axelrod, 1941). Late Cenozoic elimination of ecotypes presumably has left the high-montane species surviving in habitats which may be considerably different from those occupied by certain of their close fossil relatives.

During Alvord Creek time the distribution of vegetation over the rolling hills and wide basins seems to have been controlled largely by slope exposure and

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to a lesser extent by elevation. Judging from their abundance as fossils, *Acer, Amelanchier,* and *Rhus* are considered to have dominated at the site of deposition. Drier exposed slopes about the lake basin supported a woodland-chaparral community of *Arbutus, Ceanothus, Cercocarpus, Juniperus,* and *Photinia.* The climate seems to have been sufficiently arid to permit this group to approach the site of deposition on more exposed slopes, so that certain species, notably *Cercocarpus,* entered accumulating sediments in appreciable numbers. A *Pseudotsuga-Pinus-Abies* association occupied the cooler slopes and moister valley bottoms, with associates of *Acer, Amelanchier, Rosa,* and *Rhus.* In this forest were species of *Carpinus* and *Prunus* whose nearest relatives now survive in the eastern United States and eastern Asia. Upland species of *Abies, Picea, Populus, Pinus,* and *Sorbus,* which presumably formed a forest zone on the flanks of volcanoes several miles distant, extended toward the Alvord Creek basin along cold streams and cooler slopes so that their leaves, seeds, and cone scales occasionally entered accumulating sediments.

A general index to Alvord Creek climate is provided by the present climate of the inner north Coast Ranges and adjacent Klamath Mountain area of California. All the dominants in the flora are represented here by closely related plants, and a majority of the fossil species have equivalents in the region. At Shasta Valley on the leeward slopes of the Klamath Mountains there is a complete overlapping and intermingling of Upper Sonoran and Arid Transition communities. *Acer macrophyllum,* which reaches its inland limits of distribution in this area, has deeply lobed leaves which resemble the fossil *A. alvordensis. Amelanchier* is common along stream banks, much as it appears to have been during Alvord Creek time, and *Ceanothus, Cercocarpus,* and *Juniperus* are scattered over the slopes near at hand. The Sierra-Cascade forest descends from higher elevations into this Upper Sonoran zone at Shasta Valley, where rainfall ranges from 18 to 23 inches yearly. On the slopes above, where rainfall is from 5 to 10 inches greater, the forest includes such species as *Abies concolor, A. shastensis, Pseudotsuga taxifolia,* and their common associates. *Picea breweriana* has been reported from this area, as previously mentioned.

Various oaks are abundant in this region today, but *Quercus* has not been recorded at Alvord Creek. Further collections may reveal the fossil equivalents of such species as *Quercus chrysolepis, Q. garryana,* and *Q. kelloggii,* but it seems certain that they had a limited occurrence in the area. The absence of such oaks from the Alvord Creek flora is difficult to explain from a climatic standpoint. Although they are limited at the interior today by low winter temperatures, this can hardly have been a factor accounting for their absence at Alvord Creek. The flora contains a number of species, in such genera as *Ceanothus, Cercocarpus, Amorpha,* and *Photinia,* whose equivalents survive in regions where winters are mild and where oaks are characteristic. There are other floras in the Great Basin area, aside from the Alvord Creek, that show essentially the same relations. Among several thousand leaves in the Lower Pliocene Verdi flora of western Nevada there are only 4 oak specimens; they are battered and apparently were transported into the basin of deposition from

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more distant slopes. Oaks are equally rare in the near-by Chalk Hills flora, which is represented also by numerous other specimens. Since both floras contain a large number of species whose equivalents are common today in central and southern California where oaks are dominant and winters mild, it is difficult to imagine the climatic factors which might account for their absence here. Curiously, the essentially contemporaneous Esmeralda flora 130 miles southeast contains a number of oaks (Axelrod, 1940*a*), and the transitional Mio-Pliocene Fallon flora 40 miles east is dominated by *Quercus*. It may be recalled that Chaney and Elias have commented on the absence of oaks from the High Plains floras, since in equivalent flood-plain vegetation 100 to 150 miles eastward they are common (1936). It is significant that a recently collected flora from a probable Pliocene horizon in northern Texas contains numerous oaks (Chaney, oral communication, April 1942). Oaks have not been recorded in the transitional Mio-Pliocene Neroly flora of west-central California (Condit, 1938), which otherwise shows close relationship to modern forests in the eastern United States, where oaks are predominant.[8] Yet in a flora which was discovered recently in strata directly underlying the Neroly at Corral Hollow, both live oaks and deciduous oaks are not infrequent.

The climate of the Shasta Valley area approximates that of Alvord Creek time, since it represents conditions expressed by the majority of the species and dominants of the flora. Nevertheless, it is clear that the Alvord Creek species whose nearest equivalents do not live in this region also have definite climatic significance. Their presence in the flora indicates that the physical conditions of Alvord Creek time must have differed in some respects from those now found about the borders of Shasta Valley. Two significant plants not now represented there are *Amorpha californica* and *Photinia arbutifolia,* common shrubs in the Arid Transition and Upper Sonoran zones south of Mount Shasta. As related to an interpretation of Alvord Creek conditions, their significance seems to lie in the fact that they do not range into areas whose average yearly temperature is much below 57° or 58° F. Their distribution at the north apparently is limited by winter cold, and particularly by temperatures falling below freezing for any length of time. Four Alvord Creek species, *Abies alvordensis, Carpinus grandis, Picea sonomensis,* and *Prunus harneyensis,* are relicts of the East American and East Asian Elements which characterized the Miocene forest of the northern Great Basin. Their subordinate role at Alvord Creek, in contrast with their dominance in the Miocene, implies a lowered total rainfall, a decrease in the amount of summer precipitation, and higher summer temperatures. *Arbutus idahoensis* and *Cercocarpus holmesii* are members of the Conifer woodland and Chaparral Components whose nearest descendants now live under a climate of moderate rainfall distributed as summer showers and winter rains. The rarity or absence of such species in the earlier Miocene floras, and their increased abundance in the later Miocene and early Pliocene floras of this region, suggest that conditions favorable for their growth near sites of deposition

[8] There is a specimen of *Quercus convexa* Lesquereux in the Neroly collections at the U. S. National Museum from Corral Hollow.

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prevailed here only in late Tertiary time. As they become more abundant at the north, the East American and East Asian Elements, and also the mesic Redwood and North-coast coniferous Components, show a reduction in numbers. The appearance of these semiarid members of the Madro-Tertiary Flora in the northern Great Basin is thus considered to be a reflection of lowered precipitation, increased extremes of temperature, and concentration of rainfall into the summer and winter months.

It is evident that the fossil plants having living representatives in regions away from the Shasta Valley area modify to some extent the climatic aspects of the Alvord Creek flora as they might be gauged from a consideration of conditions at Shasta Valley alone. Climatic conditions in Alvord Creek time appear to have been essentially as follows: Annual rainfall over the lower basin probably was about 20 to 23 inches, increasing in the adjacent hills to about 28 or 30 inches. Precipitation at this time was distributed as summer showers and winter rains. The greatest amount probably was received during the winter season, judging from the poor representation of members of the East American and East Asian Elements. Temperatures were mild, with moderate ranges of extremes. The yearly average temperature is thought to have been in the neighborhood of 57° or 58° F. over the lower basin, and somewhat lower in the bordering hills. The average maximum temperature for the hottest summer month may have been near 85° F., with the average minimum for the coldest winter month about 20° F. The extremes of high and low over the lower basin may have reached 110° and 0° F., respectively. These figures, which have been estimated on the basis of conditions existing in areas where vegetation shows greatest relationship to the fossil flora, agree closely with conclusions already reached by Dorf for early Pliocene climate in the northern Great Basin (1936, p. 97).

The postulated Alvord Creek climate is in marked contrast with that at the fossil locality today. Rainfall over the lower Alvord basin averages 9 or 10 inches yearly. Precipitation falls mostly during the winter months, and, depending largely on elevation, the higher mountains may receive 20 to 40 inches of snow. There is a secondary maximum during spring, and occasional showers may occur at higher levels in the summer months. But this rainfall is lost largely by rapid evaporation resulting from the high summer temperatures. On the basis of temperature data recorded at Andrews, 18 miles south of Alvord Creek, and at Juniper Ranch, 23 miles north at essentially the same elevation, the average annual temperature at Alvord Creek is estimated at about 47° F. From data for the same stations, the average July maximum is estimated to be near 90° F. and the average January minimum approximately 17° F. The highest temperature recorded in the area is in the neighborhood of 106° F., and the lowest is about −35° F.

From these data it may be concluded that rainfall today is fully 10 inches below that of Alvord Creek time. Likewise, there now is insufficient summer precipitation for the modern representatives of 7 species in the flora. Important temperature changes in this area have involved a lowering of the average an-

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nual temperature about 10° F., and the summer and winter extremes reach considerably above and below those of the Alvord Creek stage.

Summarizing the evidence for the physical setting and vegetation in the Alvord Creek area during the deposition of the flora, the following points may be listed:

1. The fine-grained character of the leaf-bearing shales, the nature of the associated deposits, and the mode of plant preservation, all suggest deposition in a small lake surrounded by a region of moderate topographic diversity with volcanic cones a few miles distant.

2. A rosaceous shrub community and deeply lobed *Acer* of the *macrophyllum* type occupied the lake border. Species of *Ceanothus, Cercocarpus, Photinia,* and *Juniperus* inhabited more exposed slopes about the basin and in certain areas approached the lake. A *Pinus-Abies-Pseudotsuga* community and its regular associates lived on cooler slopes near at hand, and here also were a few species whose nearest equivalents now survive in eastern Asia and eastern North America. In the upper parts of this forest, and extending to lower levels on sheltered slopes, were montane species of *Abies, Picea, Pinus, Populus,* and *Sorbus,* which contributed only occasional material to the sediments.

3. Annual rainfall over the immediate basin was in the neighborhood of 20 to 23 inches, or about 10 inches greater than that of today. Precipitation in Alvord Creek time increased to 28 or 30 inches in the upper parts of the near-by montane forest. Rainfall appears to have been distributed as winter rains and summer showers. Seasonal temperatures were more moderate in Alvord Creek time than today, with the average yearly temperature about 10° F. higher than at present.

Age of the Flora

In determining the age of the Alvord Creek flora, two major lines of evidence will be considered: first, the distribution of its species in other floras of known age,[4] and second, the climatic and floral character of the Alvord Creek as compared with Miocene and Pliocene floras near at hand.

All the 25 woody plants in the flora, except *Abies alvordensis, Pinus alvordensis, Prunus harneyensis,* and *Rhus alvordensis,* occur as identical or related species in Miocene and Pliocene floras in the western United States, as listed in table 23. There are 8 identical and 5 related species in the Middle and Upper Miocene floras of the northern Great Basin and Columbia Plateau; 6 identical and 2 related species in the transitional Mio-Pliocene floras of southwestern Idaho and central California; and 9 identical and 3 related species in Pliocene floras of California, Oregon, and Nevada. The Alvord Creek species related to those in the Miocene are highly suggestive of its younger age, since they show a trend toward smaller leaf size in response to increased aridity in this area in post-Miocene time. In all cases the related species of *Acer, Amelanchier, Arbutus,* and *Populus* which occur in the Miocene have leaves of greater dimen-

[4] Excluded from consideration is *Potamogeton* sp., for like most aquatics it has no close stratigraphic value.

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TABLE 23

STRATIGRAPHIC DISTRIBUTION OF ALVORD CREEK SPECIES

SPECIES (Total, 21)	MIOCENE: MIDDLE AND UPPER: Latah	Mascall	Succor Creek	Blue Mountains	Upper Cedarville	Payette	Trout Creek	TRANSITIONAL: Lower Idaho	Remington Hill	Table Mountain	PLIOCENE: LOWER: Verdi	Esmeralda	Creede	Troutdale	MIDDLE: Deschutes	Alturas	Mulholland	Oakdale	UPPER: Sonoma	Santa Clara
Abies klamathensis		x																		
Acer alvordensis	o	o	o	o	o		o	o												
Amelanchier alvordensis	o	o					o										o			
Amorpha condoni														x					x	
Arbutus idahoensis	x	x	o	o		x	o	x		?										
Carpinus grandis							x													
Ceanothus precuneatus									x		x							x	x	
Cercocarpus antiquus										x		o					o			
Cercocarpus holmesii													x							
Juniperus alvordensis								x												
Mahonia reticulata			x	x			x													
Photinia sonomensis																	x	x	x	
Picea lahontense							x													
Picea sonomensis				x		x		x											x	
Pinus sp.			?	?							x									
Populus payettensis						x					x					x				
Populus pliotremuloides		o		o		o	o		x		x	x			x	x		x	x	
Pseudotsuga sonomensis							o	o					x						x	x
Rosa alvordensis							o													
Salix payettensis						x														
Sorbus harneyensis													o							
Identical species	1	2	1	2	0	4	3	3	2	1	4	1	2	1	1	2	1	3	6	1
Related species	2	3	2	3	1	1	6	2	0	0	0	1	1	0	0	0	2	0	0	0
Identical species in stage				8					6				7				4		6	
Related species in stage				5					2				2				2		0	
Identical species in epoch				8					6								9			
Related species in epoch				5					2								3			

x = identical species; o = related species.

sions, and also of shallower lobation in the case of *Acer*, than the Alvord Creek species. The paleobotanical bases for differentiating such species have already been presented by Chaney (1938*a*, pp. 212–213), and the reader is referred to this discussion for a detailed statement. In each instance one modern equivalent plant includes two fossil species within its normal range of leaf variation. For example, both the Miocene *Acer bendirei* and the Pliocene *A.*

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alvordensis are related to *A. macrophyllum*. The Miocene species most closely resembles leaves produced by the modern maple in the humid and coastal parts of its range, and the Pliocene species resembles leaves formed by that species in the semiarid and southern parts of its distribution. This trend toward smaller-leafed species in the northern Great Basin from Miocene to Alvord Creek time is interpreted as a reflection of lowered rainfall here following the Miocene, and is therefore an indication of its Pliocene age.

Such criteria for age evaluation must be used with the understanding that middle and later Tertiary floral history differs in the several provinces of the western United States. It is possible to have such species as *Populus alexanderi* Dorf and *P. pliotremuloides* Axelrod in the Miocene Tehachapi flora of the Mohave region because semiarid or "Pliocene" conditions prevailed there during that stage (Axelrod, 1939, p. 62). Since a semiarid climate developed in central Nevada before it appeared in the northern Great Basin and adjacent areas, leaf species of Pliocene types may occur in the Upper Miocene of west-central Nevada, but do not appear in the northern Great Basin until the end of that stage and in the Pliocene. Likewise, they occur in west-central California at a still later date, because humid conditions lasted longer in that area than in the Great Basin province (Axelrod, 1940*b*, pp. 484–486). Significantly, these relations are similar to those shown in the northward dispersal of the Madro-Tertiary Flora (Axelrod, 1939). Appearing at the south in early Miocene time, this semiarid vegetation gradually spread northward as conditions became drier, establishing itself as an important unit in the central Great Basin by the Upper Miocene, and in the northern Great Basin late in that stage and in the early Pliocene. Its later appearance in central California has been explained by the persistence of humid conditions for a longer time in that area. It is apparent that with the rapid expansion of semiarid conditions in the western United States during Upper Miocene and Pliocene times, many members of the northern forest developed smaller and thicker-textured leaves, and that these "Pliocene" leaf forms often occur with members of the Madro-Tertiary Flora. An equally significant change, discussed below, is the gradual reduction in numbers of the Redwood and North-coast coniferous Components of the West American Element, as well as the East American and East Asian Elements, as the Madro-Tertiary Flora ranged northward and coastward in the late Tertiary.

Table 23 shows that 9 identical and 3 related species occur in the Pliocene of the western United States. Eight of the Alvord Creek species, *Amorpha condoni, Ceanothus precuneatus, Cercocarpus antiquus, C. holmesii, Juniperus alvordensis, Photinia sonomensis, Pinus* sp., and *Sorbus harneyensis,* are not recorded certainly below the Mio-Pliocene transition in the northern Great Basin. One of them, however, *Pinus* sp., may be represented by certain Miocene records of *Pinus knowltoni* Chaney, and the *Sorbus* would find an ecological position in several of these floras.[5] Four of the Alvord Creek species which are not certainly known from the Miocene of the Great Basin and Columbia

[5] *Sorbus alvordensis* MacGinitie (1933) from Trout Creek apparently is not rosaceous (see p. 259).

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Plateau, *Ceanothus precuneatus, Cercocarpus antiquus,*[6] *Photinia sonomensis,* and *Amorpha condoni,* are represented by identical or related species in the Miocene of southern California (Axelrod, 1939). They are semiarid members of the Madro-Tertiary Flora which projected its range northward into the Columbia Plateau only in the latest Miocene and early Pliocene. The Alvord Creek *Juniperus alvordensis* and *Cercocarpus holmesii* are also considered to belong to this group. Their rarity in or absence from the Middle and Upper Miocene floras, and their rather common occurrence in the Alvord Creek flora, suggest its post-Miocene age.

The age of the Alvord Creek flora may be estimated more closely by comparing it with adjacent Miocene and Pliocene floras from the standpoint of its floral and climatic character. The Miocene floras nearest to Alvord Creek are the Trout Creek 30 miles southeast (MacGinitie, 1933), the Upper Cedarville 110 miles southwest (LaMotte, 1936), and the Succor Creek 90 miles northeast (Brooks, 1935; Smith, 1938*b*). There are sufficient resemblances between these floras to show that they represent a similar type of forest, and to suggest that although there may be slight differences in age between them, these cannot be great. These floras lived under an annual rainfall of from 35 to 50 inches well distributed throughout the year, and under moderate ranges of temperature. By contrast, the Alvord Creek flora lived in this region at a time when rainfall was fully 15 inches lower and distributed as summer showers and winter rains, and when seasonal extremes of temperature were greater. In view of the well established trend toward lowered precipitation and increasing extremes of temperature in this region during the Tertiary, it follows that the climatic change from Middle and Upper Miocene time to the Alvord Creek stage is sufficient to indicate that the Alvord Creek is no older than Lower Pliocene.

As a result of its more continental type of climate, the Alvord Creek flora has only a few members of the East Asian and East American Elements which characterized the Middle Tertiary floras of this region. Typical genera of these elements in Miocene floras closest to Alvord Creek include the following:

Ailanthus	Diospyros	Nyssa
Carpinus	Fagus	Sassafras
Carya	Ginkgo	Taxodium
Castanea	Glyptostrobus	Ulmus
Cebatha		

Conditions suited to their optimum development were modified in the northern Great Basin in late Miocene time as rising barriers at the west resulted in a lower rainfall and greater extremes of temperature over the inland province. The relict occurrence of 4 species representing these elements at Alvord Creek, *Abies alvordensis, Carpinus grandis, Picea sonomensis,*[7] and *Prunus harneyen-*

[6] *Cercocarpus antiquus* and the related *C. cuneatus* have been reported from the Miocene of the northern Great Basin and Columbia Plateau. These records, however, are based on specimens which seem referable to other genera (see p. 256).

[7] *Picea sonomensis* also belongs to the West American Element.

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sis, is considered sufficient to indicate the post-Miocene age of the Alvord Creek flora.

Such an age assignment is suggested also by comparison with the Lower Idaho flora near Weiser, 125 miles northeast (Dorf, 1936; Smith, 1938*a*). The Lower Idaho differs from the Alvord Creek in having *Sequoia langsdorfii* and certain of its mesic associates. These plants are commonly represented in the Miocene of the northern Great Basin but are not known to have persisted beyond the early Pliocene, owing to increased extremes of temperature and lowered rainfall over the region by this stage. Their relict occurrence in the Lower Idaho flora is in line with its transitional Mio-Pliocene age, and their absence at Alvord Creek suggests its post–Lower Idaho age. The Lower Idaho differs also from the Alvord Creek in having a larger number of the genera representing the East Asian and East American Elements. Their small quantitative representation in the Lower Idaho, in contrast with their dominant place in the Miocene, also suggests the transitional Mio-Pliocene age of the Lower Idaho. If the Alvord Creek were essentially contemporaneous, additional members of these elements might be expected in it; their relict occurrence thus again suggests the post–Lower Idaho age of the flora. The floral and climatic changes between Idaho and Alvord Creek time seem sufficient to indicate that the Alvord Creek is Lower Pliocene, and to suggest that the flora does not belong to the basal part of that stage.

Members of distinctly drier types of vegetation became more abundant in the northern Great Basin in the later Miocene as the mesic Redwood and North-coast coniferous Components and the associated East American and East Asian Elements were reduced in numbers. This drier group includes trees and shrubs of the Border-redwood, Sierra-Cascade, and Rocky Mountain Components. They are subordinate in the early Miocene floras, but with the reduction in rainfall later in the epoch they are increasingly common. Their dominance in the Alvord Creek flora suggests that it lived subsequent to Miocene time.

In addition to these plants, Miocene floras of the northern Great Basin contain a few species whose nearest relatives now characterize woodland and chaparral vegetation in southwestern United States. With greater aridity in the northern Great Basin in the late Miocene and Pliocene, members of this Southwest American Element entered the accumulating record in increasing numbers. The Alvord Creek species *Arbutus idahoensis, Ceanothus precuneatus, Cercocarpus antiquus, C. holmesii, Photinia sonomensis,* and *Juniperus alvordensis* belong to this element. It is represented also in the Lower Idaho flora, and two species, *Arbutus idahoensis* and *Juniperus alvordensis,* are now known to occur in both floras. Additional members of this element in the Lower Idaho that have not been collected at Alvord Creek include *Pinus lindgreni* Knowlton, *Quercus declinata* Dorf, and *Q. hannibali* Dorf. The Southwest American Element has a greater representation at Alvord Creek than in the Lower Idaho, which is to be expected in view of its more arid climate. The Alvord Creek occurrence suggests that it became more abundant in this region following Lower Idaho time, but it is not possible to evaluate the exact quantitative as-

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pects of the element, owing to the incomplete Pliocene record in this region. Judging from its representation in the Esmeralda (Axelrod, 1940*a*) and Truckee floras (Axelrod, unpublished) of western Nevada, it is believed that the Alvord Creek occurrence may express its maximum development in the northern Great Basin. In any event, its greater development here than in the Lower Idaho suggests drier conditions, and hence a post-Lower Idaho age.

The climatic and floral character of the Alvord Creek expresses Lower rather than Middle Pliocene conditions in the northern Great Basin. This is indicated by a comparison with the Middle Pliocene Alturas flora 130 miles southwest in Modoc County, California, which is described in the following chapter in this volume, as well as by the Middle Pliocene Deschutes flora (Chaney, 1938*a*) 165 miles northwest in Oregon. The Alturas flora is now known to contain 7 species. Judging from the abundance of cottonwoods (*Populus alexanderi, P. payettensis*) and aspen (*P. pliotremuloides*) and the presence of three willows (*Salix*), the Alturas suggests a relatively semiarid region in which trees and shrubs were limited largely to stream banks. Since this region supported a mesic forest during Miocene time (LaMotte, 1936), the Alturas flora indicates a wide restriction of forest cover after the Miocene in response to lessening rainfall. Accompanying this trend toward aridity, certain species show gradual reduction in leaf size. The Miocene cottonwood, aspen, and elm all have larger leaves than the Alturas species. This survival of hardy derivative trees along stream banks following the restriction of the mesic Miocene forest is a regular feature of the Pliocene floras of the northern Great Basin and Columbia Plateau. Forests may have lived in the adjacent uplands, but they seem to have been so restricted that they did not contribute leaves and other structures to accumulating Alturas sediments. Annual rainfall during Alturas time probably did not exceed 12 to 15 inches.

The following comparison between the Alvord Creek and the Alturas suggests the position of the former within the Pliocene. The Alvord Creek represents border-forest conditions, whereas the Alturas is a riparian assemblage. The widespread restriction of forest cover in the northwestern Great Basin between Alvord Creek and Alturas time seems ample reason for postulating a Lower Pliocene age for the Alvord Creek. In its general climatic character the Alturas is more arid, and hence younger than the Alvord Creek. The lowering of rainfall 5 to 8 inches between Alvord Creek and Alturas time seems sufficient to indicate that the Alvord Creek is Lower Pliocene. Members of the East Asian and East American Elements have a relict occurrence at Alvord Creek, but they were completely eliminated from the lowlands of this region by Alturas time except for the hardy, small-leafed elm which persisted along stream banks. This floral change also seems sufficient to indicate that the Alvord Creek is pre-Middle Pliocene in age.

The Deschutes flora of north-central Oregon (Chaney, 1938*a*) provides additional data for interpreting the Alvord Creek. The Deschutes was laid down in a moderately upland area in close proximity to an active volcano. The dominant aspen (*Populus pliotremuloides*) and the associated cottonwood (*Populus*),

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cherry (*Prunus*), box elder (*Acer*), and willow (*Salix*) suggest a cool, semiarid climate in which trees were restricted largely to stream banks in relatively open country. Modern riparian vegetation in the near-by Ochoco and Blue mountains at elevations of from 3000 to 3700 feet, where rainfall ranges from 14 to 16 inches yearly, resembles the Deschutes assemblage. On the basis of more recent studies of Pliocene vegetation elsewhere in eastern Oregon, Chaney now considers that the flora is Middle Pliocene in age, as set forth in chapters 11 and 13 of this volume.

In his reconstruction of physical conditions during Deschutes time, Chaney has pointed out that modern vegetation in the Ochoco and Blue mountains at elevations above 4000 feet is considerably more mesic than the Deschutes flora. All living equivalent Deschutes species in eastern Oregon range upward into this zone, where precipitation is 20 inches and more yearly. They occur here, however, with *Abies grandis, Pinus ponderosa, Pseudotsuga taxifolia,* and their associates of *Alnus, Acer, Amelanchier, Betula,* and *Rosa,* none of which are known to have representatives in the Deschutes. The vegetation in this upland area is more nearly like that already described for the Alvord Creek flora. In other words, the differences between the Deschutes and Alvord Creek floras are comparable in a general way with the differences in modern vegetation occurring at different elevations in the mountains of northeastern Oregon. The Deschutes is made up of trees and shrubs whose equivalents live along stream borders well below forested country. The Alvord Creek more nearly resembles the forest occurring about 1000 feet above the zone of Deschutes living equivalent vegetation, where rainfall exceeds by 5 or more inches that of the zone below.

It is apparent that the lowering of rainfall 5 to 8 inches yearly in eastern Oregon between Alvord Creek and Deschutes time was sufficient to restrict forests into upland areas away from sediments accumulating in low to moderately upland habitats. The vegetation of the later stage largely represents derivative Miocene trees and shrubs which survived along stream borders at lower levels in semiarid open country. This change, which is similar to that already discussed for the Alturas, seems ample to indicate the Middle Pliocene age of the Deschutes as well as the Lower Pliocene age of the Alvord Creek flora.

The foregoing data which have a bearing on the age of the Alvord Creek flora may be summarized as follows:

1. The flora is dominated by species which differ from their nearest Miocene relatives in having leaves of deeper lobation or of smaller size and thicker texture. In view of the well known trend toward increased continentality in this region during the middle and later Tertiary, their occurrence at Alvord Creek indicates its post-Miocene age.

2. The floral composition and climatic relations, which are intermediate with respect to Upper Miocene and Middle Pliocene floras in the northern Great Basin and Columbia Plateau, suggest a Lower Pliocene age.

It may be added that available evidence not only points to the Lower Pliocene age of the Alvord Creek flora, but suggests also that it probably represents the earlier rather than the later half of that stage.

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This early Lower Pliocene age assignment of the Alvord Creek flora has an important bearing on the ages of associated formations in the Alvord Creek region. The Alvord Creek formation, which has been variously considered to be as old as Mascall (Wilmarth, 1938, p. 43) and possibly as young as Lower Pliocene (Fuller, 1931, p. 115), is overlain by volcanics which have a wide areal distribution in the adjacent area. The Steens basalt, which has a maximum thickness of about 3000 feet, is separated from the Alvord Creek formation by the Pipe Creek volcanics (1500 feet) and the Steens Mountain andesite (1500 feet). Fuller has shown that the Steens basalt extends southward as almost continuous exposures from Alvord Creek to Pueblo Mountain on the Oregon-Nevada boundary (1931, p. 105). At the southern end of Pueblo Mountain the Steens basalt dips conformably beneath the Thousand Creek beds (Fuller, 1931, p. 105), which contain a large mammalian fauna that is now considered to represent the later part of Middle Pliocene time (Wood *et al.*, 1941, table). It follows that the upper part of the Steens basalt is essentially of Thousand Creek age. Since the Alvord Creek represents early Lower Pliocene time, it would appear that the Pipe Creek volcanics and Steens Mountain andesite may have been deposited in the later half of the Lower Pliocene, with the first extrusions of Steens basalt commencing at the end of Lower Pliocene or at the beginning of Middle Pliocene time.

In connection with this evidence for the early Middle Pliocene age of the Steens basalt, it is desirable to review the relations of that formation in the Warner Lake region, 40 miles west of Steens Mountain and separated from it by Clayton and Guano valleys. Fuller has shown that three formations are exposed on a high scarp in the northern Warner Lake area (1931, p. 112). The lower 1000 feet of basalt flows are considered to represent the Steens basalt, and these are overlain by approximately 300 feet of tuffs which are capped by an upper basalt 400 feet in thickness. This upper basalt has been interpreted as the Warner basalt of the Warner Mountains of northeastern California, 40 miles south. Following Russell's suggestion (1928, pp. 439–440), Fuller was inclined to regard the tuffs underlying the Warner basalt in the Warner Lake area as part of the Upper Cedarville formation, which underlies the Warner basalt in the Warner Mountains at the south (1931, p. 113). Fuller (*ibid.*, p. 114), citing Russell (1928, p. 412), states that vertebrates of later Tertiary age have been found in the Upper Cedarville, and on this basis he considered the Steens basalt to be of late Miocene or Lower Pliocene age. It must be pointed out, however, that mammalian remains are not known from the Upper Cedarville, whose Middle to Upper Miocene age is well established by a large flora (LaMotte, 1936). LaMotte has already shown that the vertebrates cited by Russell and Fuller are from the Alturas formation, which unconformably overlies the Upper Cedarville in northeastern California (1936, p. 104). Thus it seems probable that the tuffaceous beds overlying the Steens basalt in the Warner Lake area are to be correlated with the Thousand Creek formation, which also overlies the Steens basalt in the area 40 miles eastward.

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Summary

The Alvord Creek flora of 26 species comes from the Alvord Creek formation at the eastern base of central Steens Mountain, southeastern Oregon. The majority of the plants find relationship with the Sierra-Cascade forest and its contiguous chaparral and high-montane associations in northern California, which are distributed through several thousand feet in elevation. A few others have relatives in eastern North America, eastern Asia, and the southwestern United States.

The flora is considered to have lived in a region of moderate topographic diversity where lake-border, conifer woodland, chaparral, forest, and upland conifer associations adjusted themselves with respect to exposure and elevation about the basin of deposition.

Alvord Creek climate was characterized by an annual rainfall of from 20 to 30 inches, distributed as summer showers and winter rains. Temperatures were high in summer and reached below freezing in winter. These conditions are intermediate between the moister and milder climate of the Miocene and the drier and colder climate of the region today.

Comparison with near-by Miocene and Pliocene floras demonstrates the Lower Pliocene age of the Alvord Creek flora.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class GYMNOSPERMAE
Family PINACEAE

Abies alvordensis new species

(Plate 42, figures 5, 8, 10, 11)

Description. Seeds 1.4 to 1.7 cm. long; the seed long oval, narrowing below and rounded above; the wing relatively small, orbicular above the seed, and strongly asymmetrical, connected to the seed in the upper half and sharply truncated, not flanking the seed.

Discussion. These fir seeds are not uncommon in the flora and may easily be distinguished from the larger, wedge-shaped, and asymmetrically cuneate *Abies concoloroides* Brown and *A. klamathensis* Axelrod. Some of the smaller seeds of *A. concoloroides* superficially resemble *A. alvordensis,* but they differ in that the wing flanks the seed in *A. concoloroides,* instead of being truncated in the upper part. Relationship may also be found with the seeds of *A. chaneyi* Mason (1927).[8] The wing of *A. alvordensis,* however, is asymmetrical, with its greatest width at right angles to the point of seed attachment, whereas *A. chaneyi* has a narrow wing that is elongated in the plane of the seed; also, the wing flanks the seed in *A. chaneyi,*

[8] Brown (1940, p. 353) places the seeds of *A. chaneyi* in synonymy with *Cedrela oregoniana.* Examination of the type and supplementary material shows conclusively that they are *Abies,* not *Cedrela.*

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instead of being truncated above. Another important point of difference is that the seed of *A. chaneyi* is slender, rather than oval.

Among modern species of the genus, *A. alvordensis* seems most nearly related to certain Asiatic firs, notably *A. recurvata* Masters (see material in University of California Herbarium).

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2078, 2079, 2080, 2081.

Abies klamathensis new name

(Plate 42, figures 6, 7, 9, 12, 13)

Abies magnifica var. *shastensis* Lemmon. Mason, Carnegie Inst. Wash. Pub. 346, V, p. 150, pl. 4, figs. 5, 6, 1927.

In view of their Tertiary age, and in accordance with accepted paleobotanical procedure, a new name is applied to our specimens and to identical cone scales described by Mason from the Mascall.

Description. Cone scale broadly oblong, 2.4 to 2.9 cm. wide and 1.2 to 1.4 cm. high; stalk 0.8 to 1.0 cm. long; base of scale subcordate, sometimes with an appendage-like flange on the lower side; bract low pyramidal, 4 mm. wide and 4 mm. high.

Seeds 2.0 to 2.4 cm. long, generally wedge-shaped in outline; the seed long oval, greatest width in upper part, 0.9 to 1.1 cm. long; the wing flanking the seed and terminated in the upper half of the seed.

Discussion. This material resembles the seeds and scales with attached bracts produced by the living *Abies shastensis* Lemmon. The Shasta fir has a discontinuous distribution from northern California and adjacent Oregon to the southern Sierra Nevada. Although it occurs commonly in the upper part of the Transition forest, it may descend well into that zone in favorable areas.

The scale figured by Mason from the Mascall flora as *Abies magnifica* var. *shastensis* (Mason, 1927, pl. 4, fig. 6) has recently been placed by Brown in synonymy with *A. chaneyi* Mason (Brown, 1940, p. 347). Brown is of the opinion that the tip of the bract has been broken off and that it would otherwise be attenuated like *A. chaneyi.* Examination of the type specimen of this scale and attached bract, and comparison with the type and supplementary material of *A. chaneyi,* lead the writer to the conclusion that they are different, as Mason originally pointed out. The bract of *A. klamathensis* from Mascall and Alvord Creek is low pyramidal, whereas that of *A. chaneyi* is acuminate. These scales closely resemble in shape those of the modern *A. shastensis,* which vary in width and length according to position on the cone. As gauged from additional Mascall material, the seed figured by Mason (1927, pl. 4, fig. 5) also seems to belong here rather than with *A. concoloroides,* as suggested by Brown (1940, p. 347).

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2082, 2083, 2084, 2085, 2086; no. 2087.

Picea lahontense MacGinitie

Picea lahontense MacGinitie, Carnegie Inst. Wash. Pub. 416, II, pp. 46–47, pl. 3, figs. 4, 6, 8, 1933.

This species is represented in the Alvord Creek flora by 2 seeds that are similar to Trout Creek material, and to those of the living *Picea engelmannii* Engelmann. This montane conifer has a wide distribution in western North America, ranging from British Columbia southward through the Rocky Mountains into Arizona, and through

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the Cascades into the Mount Shasta region of northern California, 160 miles southwest of Alvord Creek.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2088, 2089.

Picea sonomensis Axelrod

(Plate 42, figures 2, 3)

Picea sonomensis Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 190–191, pl. 36, fig. 2, 1944 (see synonymy).

Several seeds in the Alvord Creek flora are exactly like those recorded in near-by Miocene floras under such genera as *Pinus, Picea,* and *Pseudotsuga,* and also resemble the Sonoma material. As was pointed out in chapter 7 of this volume, *Picea sonomensis* shows relationship to the seeds of the modern *P. breweriana* of the Klamath Mountain region of northern California, as well as to those of several Asiatic species.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2090, 2092; nos. 2091, 2093, 2094.

Pinus alvordensis new species

(Plate 42, figure 4)

Description. Seed exceeding 1.5 cm. in length, slender; the actual seed oval, 5 mm. long and 2 mm. wide, attached to the wing at an acute angle; the wing long and slender, up to 1.0 cm. preserved, widest just behind the point of attachment to the seed.

Discussion. An Alvord Creek seed seems to be identical with those formed by the modern lodgepole pine, *P. contorta* Douglas, of the western United States. Though typically of high-montane distribution, this species descends into the Transition zone in deep canyons with cold-air drainage. On the north coast of California ecological variants of the montane species occur in proximity to the humid redwood and north-coast coniferous forests.

The seed recorded as *Pinus* sp. Brown from Thunder Mountain (Brown, 1937*a*, pl. 45, fig. 21) may also represent lodgepole pine, but it is too poorly preserved to make positive comparison with this species possible.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2095.

Pinus sp.

The basal part of a cluster of 3 needles is represented in the Alvord Creek collection. It compares closely in size with the fascicles produced by the modern western yellow pine, *Pinus ponderosa* Douglas. Until someone can critically study all the fossil pine material in the middle and later Tertiary floras of the western United States, and present a satisfactory basis for the disposition of fascicles of this type, needless duplication of names will continue to take place.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2096.

Pseudotsuga sonomensis Dorf

(Plate 42, figure 1)

Pseudotsuga sonomensis Dorf, Carnegie Inst. Wash. Pub. 412, I, pp. 72–73, pl. 6, figs. 2–4, 1930.

Twigs with attached needles in the Alvord Creek flora are like those produced by the modern *Pseudotsuga taxifolia* (Lambert) Britton of the western United States.

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The relationship between this species and the Trout Creek *Pseudotsuga masoni* MacGinitie (1933, p. 47, pl. 3, figs. 1–3) is not clear. It is discussed on page 191 of this volume. It must be noted, however, that a cone of *Pseudotsuga* has been recorded at Trout Creek (Arnold, 1935). *Pseudotsuga taxifolioidea* Arnold apparently does not differ from the cones of *P. sonomensis* recorded by Dorf in the Sonoma flora. Whereas the Trout Creek cone is closed, owing to burial in water, the Sonoma cones are open, as might be expected from the subaerial character of the Sonoma tuffs at the Petrified Forest locality.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2097; no. 2098.

Family CUPRESSACEAE

Juniperus alvordensis new species

(Plate 43, figures 1, 2, 5)

Juniperus sabinoides Ashlee. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 109, 1936.

A small twig in the Alvord Creek flora, supplemented by larger and better-preserved specimens in the Idaho flora, forms the basis for the following description. The Idaho juniper, from the Latah formation, was identified originally as *J. sabinoides* Ashlee (1932, p. 78, pl. 1, fig. 1), but Dorf has pointed out that this species is poorly figured and that comparison is difficult (Dorf, 1936, p. 109). Even if it could be shown that the Idaho and Alvord Creek specimens were identical with the Latah *J. sabinoides* Ashlee, a new name would have to be applied since *sabinoides* already has been used for a living juniper in the southwestern United States. Under these circumstances our material is described as a new species.

Description. Terminal parts of slender twigs up to 4.0 cm. long and with an average width of 1.0 mm.; the leaves opposite, distinctly sharp-pointed, awl-like, and slender, arranged in 4 rows, and from 1.0 to nearly 1.5 mm. long.

Discussion. The Idaho and the Alvord Creek juniper clearly represent the same species, for the material from both localities shows that *Juniperus alvordensis* is characterized by slender twigs and sharp-pointed, slender leaves. Among living species relationship is to be found with *J. scopulorum* Sargent, which is characteristic of the Rocky Mountain area and ranges westward into eastern Oregon. *Juniperus alvordensis* can be distinguished from such other western junipers as *J. californica* Carrière, *J. utahensis* (Engelmann) Lemmon, and *J. occidentalis* Hooker by their stouter twigs.

The leafy twigs recorded by Knowlton from the Creede flora of south-central Colorado as *Sabina linguaefolia* (Lesquereux) Cockerell (Knowlton, 1923, p. 187) more nearly resemble *J. nevadensis* Axelrod from the Esmeralda formation (1940*a*, p. 170) than the Alvord Creek species. Both the Creede and the Esmeralda junipers are similar to the living *J. utahensis* of the western United States.

The coniferous branch figured by H. V. Smith as *Sequoia affinis* Lesquereux (Smith, 1941, p. 493, pl. 2, fig. 6) resembles *J. alvordensis,* and close examination may show that both represent the same species. In any event, the fossil is much smaller than twigs commonly produced by the Sierra redwood, with which it has been compared.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 1758 (Idaho flora); paratypes, nos. 1171 (Idaho flora), 2099 (Alvord Creek); nos. 1169, 1170 (Idaho flora).

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Class ANGIOSPERMAE
Subclass MONOCOTYLEDONES
Family POTAMOGETONACEAE

Potamogeton sp.

There are several slender leaves of an aquatic plant in the Alvord Creek flora. The total length is unknown, but the specimens reach 5 cm.; the maximum width is 5 mm. They are characterized by 4 to 5 parallel veins joined by irregular crossties which are moderately spaced, and the tips are round-blunt. These slender leaves resemble those of numerous pondweeds in North America, but their exact modern affinities are difficult to evaluate.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2100, 2101.

Subclass DICOTYLEDONES
Family SALICACEAE

Populus payettensis (Knowlton) new combination

Rhus payettensis Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 733, pl. 101, figs. 6, 7, 1898.

Celastrus lindgreni Knowlton, U. S. Geol. Surv. 18th Ann. Rept., pt. 3, p. 732, pl. 99, fig. 13; pl. 100, fig. 6, 1898.

Populus dolichophylla H. V. Smith, Amer. Midland Naturalist, vol. 25, pp. 494–496, pl. 3, fig. 5; pl. 4, figs. 1, 2, 4, 1941.

Examination of the types of *Rhus payettensis* Knowlton and *Celastrus lindgreni* Knowlton, as well as additional material represented in the Payette collections, shows that all these specimens represent the same species, and that they are assignable to *Populus*. Although Brown has placed *Rhus payettensis* in synonymy with *Fraxinus idahoensis* Brown (Brown, 1937*b*, p. 516), the character of the petiole, the nature of the marginal teeth, and the venation show that this species is *Populus*. In the discussion of *Populus dolichophylla*, Smith points out that the Payette leaves of *Celastrus lindgreni* "appear to be this species"; since the Thorn Creek specimens are indistinguishable from the Payette material, *P. dolichophylla* is placed in synonymy.

Populus payettensis shows greatest relationship to *P. angustifolia* James among living cottonwoods. This narrow-leaf cottonwood occurs typically in the central and southern Rocky Mountains, but it has a discontinuous westward distribution into Nevada and southern California. Its present occurrences in these latter areas are relicts of the late Tertiary distribution of *P. payettensis*, judging from its common occurrence in the late Miocene and Lower Pliocene floras in western Nevada.

The Alvord Creek record comprises the basal two-thirds of a lanceolate leaf having small, gland-tipped teeth which are typically populoid. In addition to its Oregon and Idaho records in the Alvord Creek, Payette, and Thorn Creek floras, *Populus payettensis* is represented in the Middle Pliocene Alturas flora of northeastern California.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2102.

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Populus pliotremuloides Axelrod

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 169–170, pl. 4, figs. 1–3, 1938.

MacGinitie has recorded an aspen in the Alvord Creek flora (1933, p. 41), but this specimen has not been located. He reports, however (oral communication, September 1939), that the specimen was small and more properly referable to *Populus pliotremuloides* than to *P. lindgreni* Knowlton. A basal leaf fragment in the more recent collection seems to be an aspen. On the basis of its small size it is readily assignable to *P. pliotremuloides*.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2103.

Salix payettensis new species

(Plate 43, figure 9)

Three leaves in the Alvord Creek flora represent the genus *Salix*, and they apparently belong to the *S. fluviatilis* Nuttall group, which has a wide distribution in the western United States. With them should probably be placed a leaf fragment from the Payette formation, described as *Myrica lanceolata* Knowlton (Knowlton 1898, p. 724, pl. 99, fig. 6).

Description. Leaves long linear, the only complete leaf measuring 6 cm. long and 5 mm. wide; acute below and blunt above; petiole heavy, up to 7 mm. preserved; midrib straight and heavy; secondaries diverging from midrib at moderate angles, somewhat irregular and wandering in their outer part; tertiaries not preserved; margin entire below, with small subsidiary teeth in the upper part of blade; texture firm.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2104; no. 2105.

Family BETULACEAE

Carpinus grandis Unger

(Plate 43, figure 6)

Carpinus grandis Unger, Synop. pl. foss., p. 220, 1845.
Chaney, Carnegie Inst. Wash. Pub. 346, IV, pp. 105–106, pl. 9, figs. 6–11, 1927.

Several leaves in the Alvord Creek flora, most of which show signs of transport from more distant areas to the immediate site of deposition, represent hornbeam. They reveal no characters by which they might be separated from leaves identified as *Carpinus grandis* in Miocene floras of the northern Great Basin and Columbia Plateau. There is perhaps reason, however, to question whether they are specifically identical with the European species. The modern species *C. caroliniana* Walter is closely similar in leaf characters.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2107; nos. 2106, 2108.

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Family BERBERIDACEAE

Mahonia reticulata (MacGinitie) Brown

(Plate 43, figure 7)

Mahonia reticulata (MacGinitie) Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 175, pl. 52, fig. 4, 1937 (see synonymy).

An excellent leaflet and its counterpart are referred to this common Miocene species of the northern Great Basin and border areas. Among living plants, the Alvord Creek specimen shows relationship to *Mahonia repens* (Lindley) Don of the western United States.

The specific name *reticulata* which has been applied to the Alvord Creek and to other specimens of similar character may be open to question. The combination *M. reticulata* (MacGinitie) Brown has been based on the Trout Creek *Clematis reticulata* MacGinitie, which has an entire margin. So far as the writer can determine, this is the only record of an entire-margined *Mahonia* in the Tertiary of the western United States. It apparently shows no gradation into the leaflets with numerous marginal teeth which have been assigned to *M. reticulata* (MacGinitie) Brown. Furthermore, no living species has been noted which produces leaflets similar to the Trout Creek specimen referred to *"Clematis reticulata"* and to the leaflets that are commonly referred to *M. reticulata*. The living *M. longipes* Standley of Mexico, however, has leaflets that are exactly like the Trout Creek *Clematis reticulata*. Although they may occasionally have minor isolated teeth, they do not resemble the fossils which have been assigned to *M. reticulata*. Further collections may well show that *Mahonia (Clematis) reticulata* is an entire-margined species related to *M. longipes*, and that the leaflets which have been placed in synonymy with *M. reticulata* represent a different species. This would add another species to the list of those from the Miocene of the northern Great Basin which have temperate Mexican affinities.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2109, 2109*a* (counterpart).

Family ROSACEAE

Amelanchier alvordensis new species

(Plate 44, figure 3)

Description. Leaves round to oval, rounded to obtuse above and below; 2.5 to 3.0 cm. long and 1.6 to 2.2 cm. wide, greatest width at or just above the middle of the blade; petiole slender, up to 3.1 cm. long but mostly about 1.5 cm.; midrib firm and straight; 8 to 11 pairs of medium-thin, alternate to subopposite secondaries, diverging from the midrib at moderate angles, looping upward, subcamptodrome in lower part, entering marginal teeth above; occasional intersecondaries weakly developed; irregular tertiaries enclosing an irregular mesh; margin entire below and toothed above; the teeth single, or occasionally double, in which case they are supplied by a bifurcation of the secondary from the lower side, dentate teeth directed forward; texture medium.

Discussion. *Amelanchier alvordensis* is closely similar to the leaves produced by the modern *A. alnifolia* Nuttall in the drier and interior parts of its range in the

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western United States. A large number of western species and varieties of *Amelanchier* have been described, but the taxonomic validity of most of them is open to question; the majority seem to be ill defined ecologic forms.

The specimens of *A. alvordensis* differ from the Miocene *A. grayi* Chaney and *A. dignatus* (Knowlton) Brown of the northern Great Basin and adjacent region in their consistently smaller size. Whereas leaves of the Miocene species commonly measure from 3.5 or 4.0 to 5.0 or 6.0 cm. in length, the later Tertiary specimens are from 2.5 to 3.0 cm. long and also have a thicker texture.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2110; nos. 2111, 2112, 2113.

Cercocarpus antiquus Lesquereux

(Plate 43, figures 3, 4)

Cercocarpus antiquus Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 37, pl. 10, figs. 6–11, 1878.

Cercocarpus antiquus, which is closely similar to the living *C. betuloides* Nuttall, is one of the commonest species in the Alvord Creek flora.

Cercocarpus has been reported by several investigators from Miocene floras in the Columbia Plateau and northern Great Basin, but all these records are open to question. The specimen identified by Oliver from the Blue Mountains flora as *C. antiquus* certainly is not typical of the species (Oliver, 1934, p. 22); it may represent a small leaf of *Fagus washoensis* LaMotte, a particularly abundant species in that flora. Brown also records *C. antiquus* from the Blue Mountains flora, but his specimen likewise differs from typical leaves of the species (Brown, 1937*a,* pl. 57, fig. 6); it may represent the terminal part of an *Amelanchier* leaf. In connection with the possible occurrence of *C. antiquus* in the Blue Mountains flora, it may be added that Chaney has recently made large collections there, and reports that no *Cercocarpus* was found among several thousand specimens examined (oral communication, September 1941). If *Cercocarpus* existed in the Blue Mountains during Miocene time, it was exceedingly rare and must have been restricted to exposed slopes away from the mesic forest which dominated sites of deposition.

Cercocarpus antiquus has been reported from the Lower Idaho flora near Weiser in southwestern Idaho (Dorf, 1936, pp. 118–119). Examination of this specimen shows that it is a small leaf of *Fagus washoensis* LaMotte. It is exactly like leaves which are shown on LaMotte's plate 9, figures 4 and 5 (1936); these leaves were originally described by LaMotte as *Sorbus chaneyi* but are now recognized as *Fagus washoensis.*

Cercocarpus cuneatus Dorf, a common California Pliocene species which differs from *C. antiquus* in its smaller size, has been reported from Thorn Creek (Smith, 1941, pl. 12, fig. 1). This specimen seems more properly referable to *Holodiscus* than to *Cercocarpus;* it is similar to a leaf figured from the Creede flora as *Phyllites* sp. Knowlton (1923, pl. 43, fig. 15).

From the available evidence it is concluded that the Alvord Creek record of *Cercocarpus antiquus* represents the first for that species in the northern Great Basin and border areas. Its Lower Pliocene occurrence here with additional members of the Southwest American Element has considerable stratigraphic significance. Whereas these species occur at the south in the Miocene, they do not appear at the north until post-Miocene time, when the climate became drier and warmer.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2114, 2115; no. 2116.

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Cercocarpus holmesii (Lesquereux) new combination

(Plate 43, figure 8)

Crataegus holmesii Lesquereux, Proc. U. S. Nat. Mus., vol. 10, p. 43, pl. 3, figs. 7–9, 1887.

Planera myricaefolia (Lesquereux) Cockerell. Knowlton, U. S. Geol. Surv. Prof. Paper 131*g*, p. 188, pl. 43, figs. 16, 17, 1923.

The following description is based on specimens of *Cercocarpus* from the later Tertiary Creede and Silver Cliff floras of Colorado, and the Lower Pliocene Alvord Creek flora.

Description. Leaves long and narrowly elliptical, tapering above and below; 2.0 to 4.0 cm. long and 5 to 7 mm. wide, greatest width usually just below the middle of the blade; heavy petiole, of moderate length or short; midrib straight and firm; numerous subparallel secondaries diverging at low angles in the upper part of the blade, and at moderate angles below, extending upward rather straight or slightly bowed; tertiaries forming a herringbone pattern next to the secondaries but becoming irregular in the intersecondary areas; margin with small subsidiary teeth in the upper half of the blade and entire below; texture coriaceous.

Discussion. Lesquereux originally pointed out that the Silver Cliff leaves resembled *Cercocarpus,* but hesitated to refer them to that genus because some of the specimens have relatively long petioles. Numerous herbarium sheets of *Cercocarpus* have been examined, and they show definitely that the petioles may be long and short on the same stem.

Cercocarpus holmesii is related to the *C. paucidentatus* (Watson) Britton group *(C. paucidentatus, C. breviflorus, C. eximinus).* The leaves produced by these species, however, average smaller than the fossils, and the teeth are suppressed to a greater degree. The manner in which the differences between *C. holmesii* and the living species may have arisen is suggested by comparison with the Florissant *Cercocarpus (Planera longifolia* var. *myricaefolia* Lesquereux, 1883, pl. 29, figs. 14–27). *Cercocarpus holmesii* is intermediate in its characters between the Oligocene and the modern species. On an average, the specimens of *C. holmesii* are smaller than the Florissant species. The Florissant leaves not only are longer and wider, but they also have a thinner texture than does *C. holmesii.* In addition, the teeth are larger and they often occur below the middle of the blade instead of being restricted largely to the upper half as in *C. holmesii.* On the other hand, leaves of members of the living *C. paucidentatus* group are smaller than *C. holmesii,* their shape is more nearly linear, the teeth are restricted mostly to the upper third of the blade, and they have a thicker texture.

From these data there seems to be evidence in this section of the genus *Cercocarpus* of gradual reduction in leaf size from Florissant time down to the present. Accompanying the development of smaller-leafed species, which seems to have occurred in response to increased aridity in the middle and later Tertiary, there is evidence also of (*a*) the gradual suppression of marginal teeth and their restriction to the upper part of the blade, (*b*) the development of slender-linear leaves from more elliptical types, and (*c*) the development of a thicker-textured leaf. Similar changes in leaf characters have been noted elsewhere among such genera as *Acer, Arbutus, Amelanchier,* and *Populus.*

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2117.

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Photinia sonomensis Axelrod

(Plate 45, figure 1)

Photinia sonomensis Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 139–140, 1944 (see synonymy and discussion).

The specimens of *Photinia* from the Miocene and Pliocene floras of California and the present material are all alike in that they may be matched by leaves of the living *Photinia arbutifolia* Lindley of California. It should be pointed out, however, that further collections at the California and Alvord Creek localities may show that the Alvord Creek toyon represents a larger-leafed species.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2118; no. 2119.

Prunus harneyensis new species

(Plate 44, figures 1, 2, 4, 8)

Description. Leaves lanceolate, elliptical or occasionally ovate, base typically acute to cuneate, rarely truncate, apex acute to long tapering; slender leaves up to 7.5 cm. long and 2.0 to 2.6 cm. wide, elliptic leaves from 5.0 cm. long and 2.3 cm. wide to 4.4 cm. long and 3.1 cm. wide; midrib firm and straight; petiole stout, up to 1.2 cm. preserved, with glands near the top; alternate secondaries often wavering and irregular, diverging at 45° to 60°, subcamptodrome; numerous intersecondaries; tertiaries irregular but trending across the blade to give a cross-percurrent effect; enclosing an irregular mesh with the nervilles ending in crossties; margin serrate, with the teeth glandular-tipped; texture firm.

Discussion. All the specimens of *Prunus harneyensis* show signs of transport from more distant areas into the immediate site of Alvord Creek deposition. Nevertheless, sufficient characters are preserved to show that this species is closely related to the living *Prunus serotina* Ehrhart of eastern North America. Relationship to the living species is shown not only by the general similarities of shape and secondary venation, but also by the numerous intersecondaries, the cross-percurrent tertiaries, the character of the finer mesh, the glandular nature of the marginal teeth, and the presence of glands on the upper part of the petiole. *Prunus virens* Standley of the southwestern United States is similar also to the fossil *P. harneyensis;* it apparently is no more than a western form of the eastern *P. serotina.*

Prunus chaneyi Condit from the Neroly flora of west-central California has been considered related to *P. serotina* (Condit, 1938, p. 263, pl. 5, figs. 4, 5). The leaves of *P. chaneyi* differ from the Alvord Creek specimens and from *P. serotina* in two major respects. In the first place, the leaves of *P. serotina* are characterized by numerous intersecondaries, and these are not present in *P. chaneyi.* Secondly, the tertiary venation of *P. serotina* is essentially cross-percurrent, whereas that of *P. chaneyi* is irregular. *Prunus chaneyi* seems more nearly related to the *P. demissa–P. melanocarpa–P. virginiana* phylad than to *P. serotina.*

Dorf reports the presence of a chokecherry in the Lower Idaho flora (1936, p. 118), where it is recorded as *Prunus rustii* Knowlton. The leaf and fruit comprising this record have been examined, and the writer is likewise of the opinion that they represent the *P. demissa* group. They cannot be assigned to *P. rustii,* however, for the types of that species represent *Alnus* (Brown, 1937, p. 170). This citation is to be placed in synonymy with *P. chaneyi* Condit.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2120, 2121, 2122, 2123.

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Rosa alvordensis new species

(Plate 44, figure 5)

Description. Leaflets oval, rounded above and below; 2.0 to 3.0 cm. (estimated) long and 1.4 to 2.2 cm. wide; petiolule short; midrib straight and firm; alternate secondaries diverging at from 60° in the lower part of the blade to 40° in the upper part, bifurcating in the outer part of the blade to supply marginal teeth, subcamptodrome; tertiaries irregular; margin biserrate, with sharp teeth directed forward; texture thin.

Discussion. Several leaflets in the flora are unquestionably those of *Rosa,* and can be distinguished from the somewhat similar leaves of *Amelanchier* by their more numerous secondaries and by the teeth, which are typically biserrate and sharp.

The Alvord Creek leaflets are distinct from those figured from the Bridge Creek flora as *Rosa hilliae* Lesquereux (Chaney, 1927, p. 123, pl. 13, figs. 8, 9; pl. 14, fig. 1); fundamental differences are apparent in both shape and margin. Likewise, the several described *Rosa* species from Florissant are more nearly related to the Bridge Creek than to the Alvord Creek species.

In such a genus as *Rosa* it is obviously not possible to indicate relationship between a fossil species and any one living plant. It is perhaps sufficient to point out that the Alvord Creek shows close relationship to a number of western species, such as *Rosa gymnocarpa* Nuttall, *R. californica* Chamisso and Schlechtendal, *R. pisocarpa* Gray, and *R. ultramontana* Watson.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2124; no. 2125.

Sorbus harneyensis new species

(Plate 44, figures 6, 7)

Description. Leaflets oblong to lanceolate, tapering above to a typically blunt apex, rounded or acute below and slightly asymmetrical; 2.4 to 5.5 cm. long and 1.0 to 1.5 cm. wide; leaflets sessile; midrib firm, straight; numerous thin, alternate secondaries, typically curving above and entering the teeth, but occasionally subcamptodrome and bifurcating, the subsidiary fork entering a marginal tooth; intersecondaries typically present and supplying teeth located between those terminated by the secondaries; irregular tertiaries enclosing an irregular mesh; margin doubly serrate; texture medium thin.

Discussion. On the basis of foliar material alone it is exceedingly difficult to separate most of the living species of *Sorbus* in western North America. Nevertheless, it is apparent that the Alvord Creek specimens show close relationship to such common western species as *S. californica* Greene and *S. scopulina* Greene. *Sorbus* is distributed widely along streams at higher elevations in the western United States, and it descends regularly into the Transition forest along cold streams and in deep, cool canyons.

This new species of *Sorbus* has been described because in the writer's opinion there is considerable doubt as to whether the Trout Creek *S. alvordensis* MacGinitie represents this genus. There is only one Trout Creek specimen (MacGinitie, 1933, p. 57, pl. 9, fig. 4), and it differs from *Sorbus* in having straight, stout secondaries and a singly serrate rather than doubly serrate margin. *Sorbus alvordensis* MacGinitie may represent a small aberrant leaf of *Quercus simulata* Knowlton, which is abundantly represented in the Trout Creek flora.

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Phyllites potentilloides Knowlton from the Huerto formation of south-central Colorado is rosaceous and may represent *Sorbus* (Knowlton, 1923, pp. 191–192, pl. 43, fig. 14). The specimen is not sufficiently well preserved, however, to be referred positively to this genus.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2126, 2127; no. 2128.

Family LEGUMINOSAE

Amorpha condoni Chaney

(Plate 45, figure 9)

Amorpha condoni Chaney, Carnegie Inst. Wash. Pub. 553, pp. 318–319, pl. 51, figs. 2–4, 1944.

Two leaflets in the flora are indistinguishable from those produced by the living *Amorpha californica* Nuttall, which ranges from north-central California southward into Baja California, reappearing in southern Arizona. The undoubted relationship of the Alvord Creek specimen to mock locust is emphasized by the small spine-like projection of the midrib, by the coarse mesh formed by the tertiaries, and by the presence of glands on the blade.

As now understood, *A. condoni* differs from *A. oblongifolia* Axelrod (1939) in having a more oval shape. It seems to occur in floras of mesic aspect, such as the Sonoma, Troutdale, and Alvord Creek, whereas *A. oblongifolia* is known in the semiarid Tehachapi flora of southern California.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2129, 2129*a* (counterpart); no. 2130.

Family ANACARDIACEAE

Rhus alvordensis new species

(Plate 45, figures 4, 8)

Description. Leaflets oblong, asymmetrical below; of variable size, one measuring 5.7 cm. long and 2.2 cm. wide, the smallest one 1.1 cm. long and 1.8 cm. wide; petiolule short; midrib straight and firm; alternate secondaries looping upward at moderate angles, passing into marginal teeth, occasionally bifurcating in the outer part and extending to the margin; occasional intersecondaries; tertiaries forming an irregular, coarse mesh; marginal teeth dentate; texture medium.

Discussion. The leaflets of *Rhus alvordensis* resemble those formed by *R. glabra* Linnaeus. This species occurs on the Deschutes River in northeastern Oregon, but is nowhere common in the Pacific region. It attains optimum development in the eastern United States, where it is a typical associate of the hardwood deciduous forests.

Among the numerous fossil species of *Rhus* described from the Tertiary of western North America, *R. coriaroides* Lesquereux (1883, pl. 41, fig. 3) from Florissant, *R. longepetiolata* (Lesquereux) Brown (Knowlton, 1923, pl. 37, fig. 9; Brown, 1934, p. 60) from Green River, and *Rhus mixta* Lesquereux (MacGinitie, 1941, pl. 35, figs. 1, 4; pl. 36, fig. 1) from Chalk Bluffs seem most nearly related to *R. alvordensis,* and all of them have been compared with *R. glabra.* The Alvord Creek leaflets average smaller than these fossils.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2133; paratype, no. 2131; no. 2132.

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Family ACERACEAE

Acer alvordensis new species

(Plate 45, figures 6, 7; plate 46, figures 1, 2)

Description. Leaves palmately 5-lobed, the 2 lower lobes subsidiary; the sinuses deep, sometimes extending almost to the top of the petiole, always more than ⅔ of the blade deep; subcordate at base; the basal lobes short, acute; the upper lateral and central lobes long acuminate; length 6.5 to over 9.0 cm. from top of petiole to apex of central lobe; width 11.0 to over 16.0 cm. (estimated); the lobes slender, from 1.0 to 2.0 cm. wide in the widest part; petiole thick, heavier below, up to 3.8 cm. long; 5 primary veins slender, diverging from top of petiole, the basal pairs at right angles to the midrib or extending downward and paralleling the central primary; secondaries looping upward at moderate angles, sometimes wavering in their course, extending along the margin for some distance, joining those above by crossties; tertiaries not preserved; margin with occasional large, subscalloped teeth, acute to blunt; texture firm.

Samaras 4.3 to over 5.0 cm. long and 1.4 to 1.6 cm. wide in the widest part of the wing, near the middle of the fruit; the lower wing margin curving sharply upward just beyond the widest part of the wing, forming a deep, rounded sinus behind the seed; line of dehiscence of seed approximately 15° to 25°; seeds oval, narrowest apically.

Discussion. This species has been differentiated from the Miocene *Acer bendirei* Lesquereux on the basis of its leaves' having consistently deeper sinuses and narrower lobes. Comparison of the Alvord Creek with Miocene specimens shows that the sinuses of the Pliocene material are normally more than ⅔ of the blade deep and may often be lobed to the base, whereas leaves of the Miocene species are lobed commonly from ½ to about ⅔ of the distance to the base of the blade.

Examination of the modern leaf material of *Acer macrophyllum* Pursh, which is considered to be the living equivalent of both *A. bendirei* and *A. alvordensis,* shows that the Alvord Creek specimens are more nearly like those found on this maple in the drier and interior parts of its range, whereas the Miocene species may be matched by leaves produced by the species in the humid and coastal parts of its distribution. As with the development of lobing in *Platanus* in the Tertiary of western North America (MacGinitie, 1937, pp. 140–141), the deep sinuses shown by these Alvord Creek specimens are interpreted as a result of greater aridity and more sunshine in the region in later Tertiary time. This trend toward deeper lobing has definite stratigraphic significance in connection with the well established trend toward aridity in this area.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2136, 2137, 2139, 2140; no. 2138.

Family RHAMNACEAE

Ceanothus precuneatus Axelrod

(Plate 45, figures 2, 3)

Ceanothus precuneatus Axelrod, Carnegie Inst. Wash. Pub. 516, p. 120, pl. 11, fig. 7, 1939.

Three specimens in the Alvord Creek collection are identified as belonging to this species, which resembles the modern *Ceanothus cuneatus* Nuttall of southern Oregon,

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California, and western Nevada. In the eastern Klamath Mountain area 200 miles southwest of Alvord Creek, *C. cuneatus* is common in the Upper Sonoran zone at the lower edge of the Transition forest.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2134, 2135.

Family ERICACEAE

Arbutus idahoensis (Knowlton) Brown

(Plate 45, figure 5)

Arbutus idahoensis (Knowlton) Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 184, pl. 59, figs. 2–4, 1937 (see synonymy).

Arbutus matthesii Chaney. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 123, pl. 3, fig. 9, 1936.

On the basis of size and shape, Brown has distinguished two species of madrone, *Arbutus idahoensis* (Knowlton) Brown and *Arbutus matthesii* Chaney. The Alvord Creek leaves compare closely with specimens of *A. idahoensis* from the Latah flora, illustrated by Brown on plate 59, figures 2–4, and abundant material more recently collected by Chaney from the Mascall. It is possible that a third species may be represented by the leaves from the Payette, Idaho, and Alvord Creek floras; the material is too meager and incomplete, however, to justify establishing a new species at this time.

The Alvord Creek madrone resembles *Arbutus arizonica* Sargent of the southwestern United States, as well as certain varieties of *A. xalapensis* Humboldt, Bonpland, and Kunth in northern Mexico.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2141.

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PLATES 40—46

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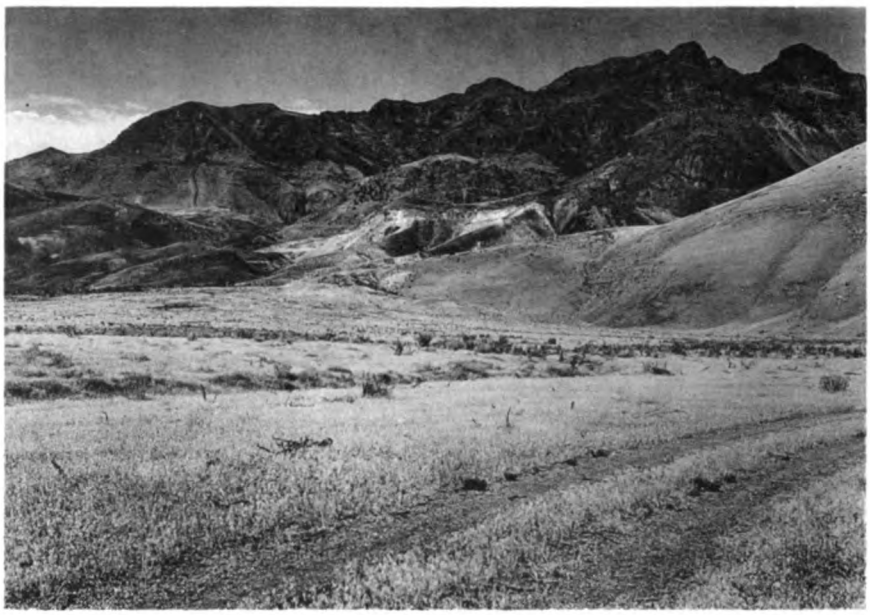

FIG. 1. Light-colored Alvord Creek tuffs exposed at base of Steens Mountain

FIG. 2. Leaf-bearing shales on south fork of Alvord Creek, locality 601

ALVORD CREEK LOCALITY

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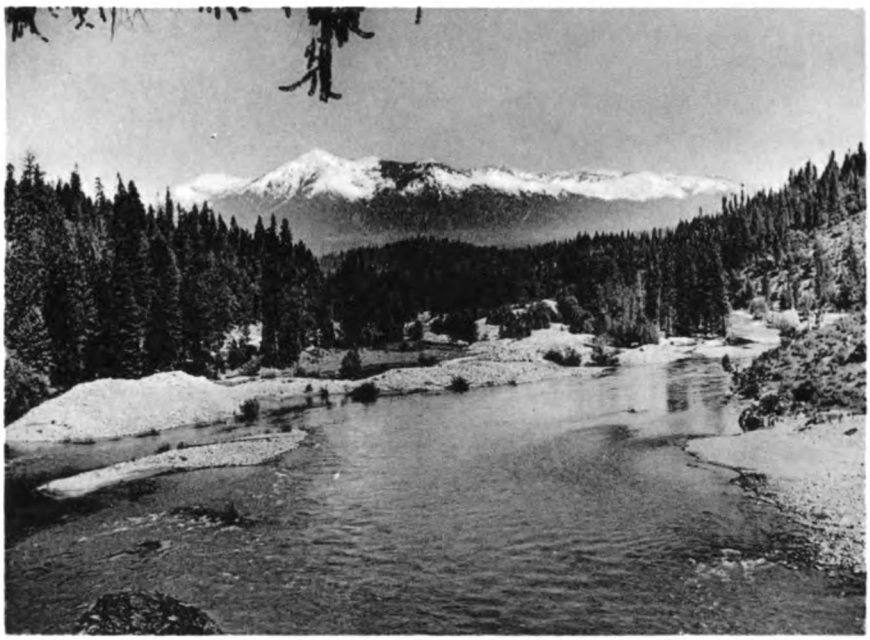

FIG. 1. Lower edge of Sierra-Cascade forest on Trinity River, with high-montane vegetation in background.

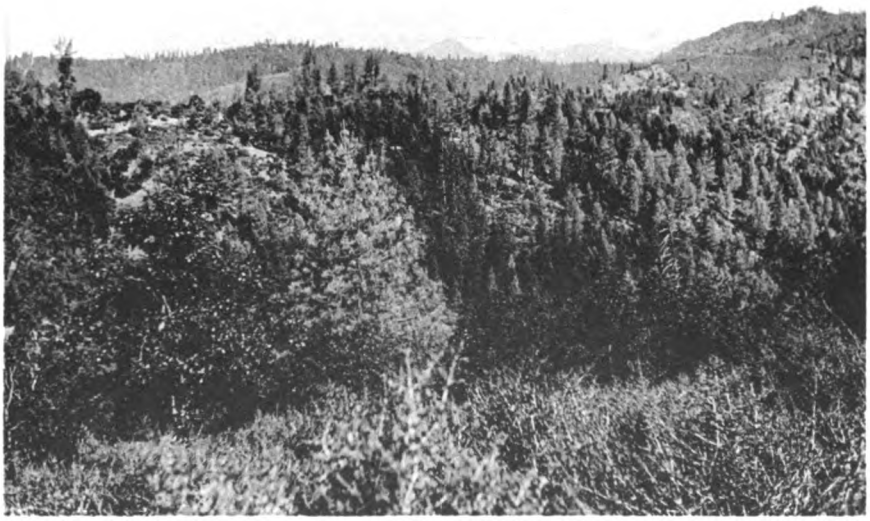

FIG. 2. Ecotone between woodland, chaparral, and forest, east of Weaverville.

LIVING EQUIVALENT ALVORD CREEK VEGETATION IN THE KLAMATH MOUNTAIN REGION

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PLATE 42

ALVORD CREEK FOSSILS

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FIG. 1. *Pseudotsuga sonomensis* Dorf. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2097 251

FIGS. 2, 3. *Picea sonomensis* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2092, 2090 251

FIG. 4. ***Pinus alvordensis*** Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2095 251

FIGS. 5, 8, 10, 11. *Abies alvordensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2078, 2080, 2081, 2079 249

FIGS. 6, 7, 9, 12, 13. *Abies klamathensis* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2085, 2086, 2084, 2083, 2082 250

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PLATE 43

Alvord Creek fossils

PAGE

Fig. 1. *Juniperus alvordensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 1758 252

Figs. 2, 5. *Juniperus alvordensis* Axelrod. Paratypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2099, 1171 252

Figs. 3, 4. *Cercocarpus antiquus* Lesquereux. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2114, 2115 256

Fig. 6. *Carpinus grandis* Unger. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2107 254

Fig. 7. *Mahonia reticulata* (MacGinitie) Brown. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2109 255

Fig. 8. *Cercocarpus holmesii* (Lesquereux) Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2117 257

Fig. 9. *Salix payettensis* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2104 254

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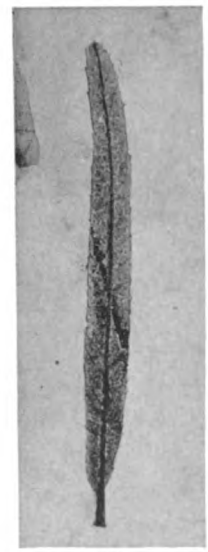

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PLATE 44

ALVORD CREEK FOSSILS

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FIGS. 1, 2, 4, 8. *Prunus harneyensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2120, 2123, 2121, 2122 258

FIG. 3. *Amelanchier alvordensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2110 255

FIG. 5. *Rosa alvordensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2124 259

FIGS. 6, 7. *Sorbus harneyensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2126, 2127 259

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PLATE 45

ALVORD CREEK FOSSILS

PAGE

FIG. 1. *Photinia sonomensis* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2118 258

FIGS. 2, 3. *Ceanothus precuneatus* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2134, 2135 261

FIG. 4. *Rhus alvordensis* Axelrod. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2133 260

FIG. 5. *Arbutus idahoensis* (Knowlton) Brown. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2141 262

FIGS. 6, 7. *Acer alvordensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2140, 2139 261

FIG. 8. *Rhus alvordensis* Axelrod. Paratype. U. C. Mus. Pal., Paleobot. Ser., no. 2131 260

FIG. 9. *Amorpha condoni* Chaney. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2129 260

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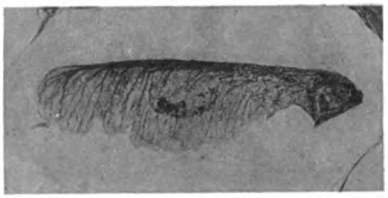

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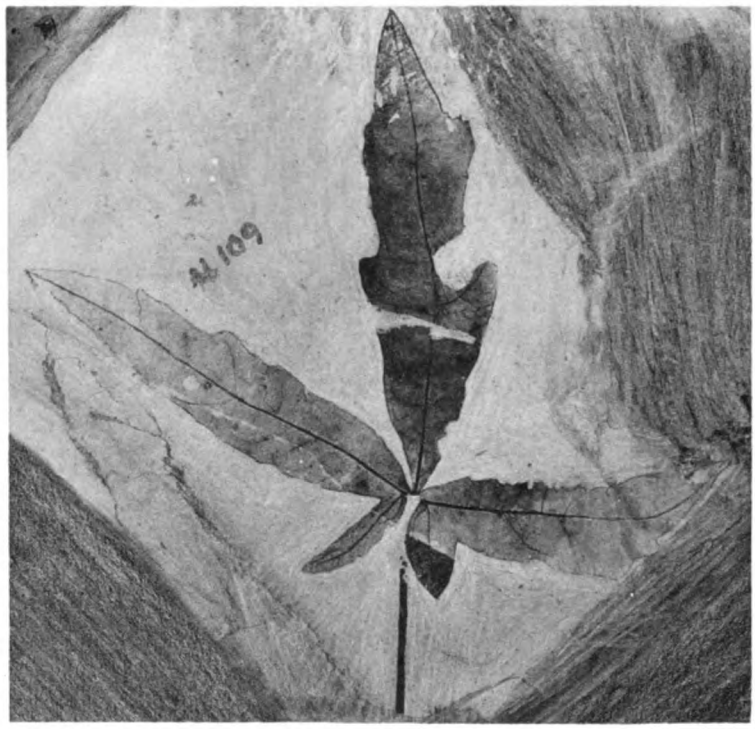

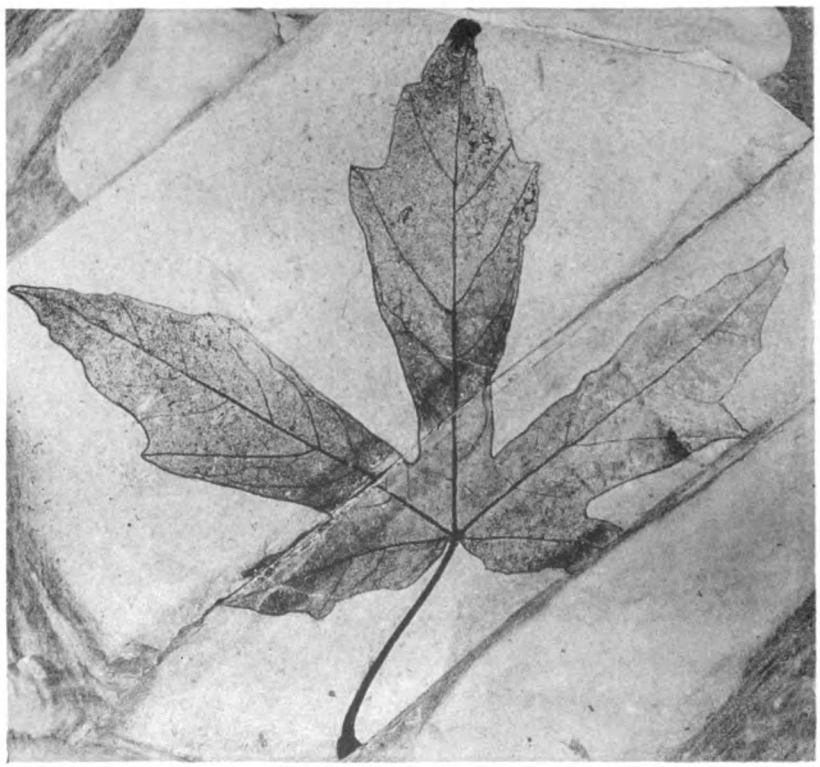

ALVORD CREEK FOSSILS

FIGS. 1, 2. *Acer alvordensis* Axelrod. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2136, 2137 . . . . . page 261

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10

The Alturas Flora

DANIEL I. AXELROD

Introduction

The Pliocene Alturas flora of northeastern California has previously been known to include only a cottonwood and a willow. Yet it occupies a position of sufficient importance among the later Tertiary floras of the western United States to have attracted the attention of three paleobotanists during the past two decades. The flora was discussed first by Chaney in his consideration of the environmental changes that took place in the northern Great Basin following Miocene time (1925*a*). He points out that the Miocene Upper Cedarville flora near Alturas represents a mesic forest that lived under an annual rainfall of from 30 to 40 inches, which was distributed rather evenly throughout the year. A more continental type of climate developed gradually over the western interior as the Coast Range, Cascade, and Sierra Nevada barriers were elevated at the west following the Miocene. By Alturas time rainfall had decreased to 15 inches yearly over the lowlands, and extremes of summer and winter temperature reached considerably above and below those of the Miocene. Only hardier species of willow and cottonwood survived along stream banks in semiarid open country during Alturas time under this new climatic regime, which was distinctly unsuited for the mesic forest of the Miocene.

The second reference to the Alturas is to be found in Dorf's monograph on the Pliocene floras of California (1930, pp. 51–52). Dorf describes *Populus alexanderi* from the Alturas collections and also reports the presence of *Salix coalingensis*. In comparison with Pliocene floras elsewhere in California, the Alturas is shown to be of significance because it illustrates the fact that the floras of this epoch vary considerably in composition, depending on their location with respect to the ocean and mountains. In differing from the coastal Pliocene floras, the Alturas clearly reflects the influence of topographic barriers which were in existence in California at this time.

Finally, LaMotte, in his discussion of the Upper Cedarville flora (1936, p. 106), uses Köppen's classification as a basis for expressing climatic change in the northern Great Basin between Miocene and Alturas time. He concludes that the Upper Cedarville flora, as well as the essentially contemporaneous Mascall, Trout Creek, and Succor Creek floras to the north and east, lived largely under a *Cfb* climate (cool mesothermal, without dry season) in lowland areas near sites of deposition. Climatic changes in this region had resulted in a *BS* climate (grassland steppe) by the Alturas stage.

In connection with the writer's studies of Pliocene floras in the western United States, the original Alturas collection has been re-examined and addi-

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tional plant material has been obtained from the Alturas formation near Rattlesnake Butte. Since the present study adds 5 species to the flora, it materially supplements our knowledge of vegetation and climate during Alturas time. These plants also permit a more complete interpretation of the floral and climatic sequence in the northwestern Great Basin during the later Tertiary than has heretofore been possible. A thorough knowledge of the succession of Pliocene vegetation in each province is now considered fundamental to a proper interpretation of these floras (Axelrod, 1940*b;* chap. 8 above). This is not only because later Tertiary vegetation varies greatly with respect to geographic position, but also because there is a rapid succession of vegetation types in the different provinces during this epoch. Only by understanding the complete later Tertiary clisere in each province can one attain an accurate concept of Pliocene plant geography in the western United States.

Geologic Occurrence

The Alturas formation of northeastern California is exposed along the Pit River valley from the vicinity of Rattlesnake Butte eastward for 10 miles to Alturas and thence northward for another 20 miles to Davis Creek (LaMotte, 1936, p. 104). The formation has a total thickness of only a few hundred feet, a figure of 355 feet being given by LaMotte for the section at Rattlesnake Butte. The relatively horizontal strata include coarse, brownish tuffaceous sandstones and pebbly conglomerates, as well as lenses of white to gray tuffaceous shales and clays. The formation rests disconformably upon the channeled and eroded surface of the Upper Cedarville formation, and is overlain regularly by the Warner basalt, of late Cenozoic age.

The Alturas flora, including the earlier collection of Alexander and Kellogg and the more recent material obtained by the writer, comes from a locality on the north bank of the Pit River about ½ mile southwest of Rattlesnake Butte (U. C. Mus. Paleobot. loc. 117). Here the comparatively flat-lying and poorly indurated strata consist largely of buff to gray tuffaceous sandstones and shales. Thin pebbly beds are not infrequent, and reworked Upper Cedarville tuff is common in the coarser deposits. Several horizons containing plant material occur in the lower part of the section, but only one of these has yielded more than fragmentary leaf impressions.

Most of the leaves are complete and well preserved, a fact which at once suggests derivation from plants living close at hand. Their frequent matted occurrence in the fine clayey lens implies accumulation in relatively quiet water. It is in this connection that the character of the leaf-bearing sediments is critical, for these finer deposits grade laterally into coarse sandstones and pebbly beds. The well rounded pebble conglomerates and the cross-bedded and current-marked finer sediments give evidence of fluvio-lacustrine deposition. These features point to a site of plant accumulation in a water body similar to the small lakes and ponds found today along the broad flood plains of many rivers. The present setting along the Pit River valley near the fossil locality is perhaps not greatly different from that of Alturas time.

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Composition and Physical Indications

The Alturas flora now comprises the 7 angiosperms listed below. All these have been reported previously from Miocene and Pliocene floras in the western United States, but two of them are here given new names for reasons presented in the systematic part of this chapter.

Systematic List of Species

Spermatophyta
  Angiospermae
    Dicotyledones
      Salicales
        Salicaceae
          Populus alexanderi Dorf
          Populus payettensis (Knowlton) Axelrod
          Populus pliotremuloides Axelrod
          Salix truckeana Chaney
          Salix vanorensis new name
          Salix wildcatensis Axelrod
      Urticales
        Ulmaceae
          Ulmus moragensis new name

Populus alexanderi Dorf, the dominant species of the Alturas flora, is now known from a number of Pliocene localities in California, Nevada, and Oregon. A study of the variation displayed by this species, as represented by abundant material in the paleobotanical collections at the University of California, shows conclusively that *P. alexanderi* resembles most closely the leaves produced by the modern *P. trichocarpa* Torrey and Gray in the drier and more southern parts of its distribution in California. In such areas the leaves of *trichocarpa,* like those of the fossil, are relatively small, essentially entire-margined, and thick in texture. It is in the more mesic parts of its range, either at higher elevations or toward the north, that *trichocarpa* leaves become larger, develop more prominent teeth, and have a thinner texture. These latter leaves resemble more nearly *P. eotremuloides* Knowlton, a common Upper Miocene species in the northern Great Basin. In commenting on the importance of this modification in leaf size and texture from Miocene to Pliocene times, Chaney states (1938*a,* p. 213): "There is expressed in this change in character of leaves, in the two latest epochs of the Tertiary, a change in physical conditions which is of fundamental significance to any understanding of the later earth history of western North America."

Populus payettensis (Knowlton) Axelrod is represented by 5 leaf impressions in the Alturas collections. This species is abundant in the Lower Pliocene Verdi flora of western Nevada and is known also from the Alvord Creek flora of southeastern Oregon, as stated in the preceding chapter of this volume. Among its Miocene localities are the Thorn Creek (Smith, 1941) and Payette (Knowlton, 1898) floras of southwestern Idaho, and the Lower Coal Valley flora of west-

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central Nevada (see collections at the University of California). *Populus payettensis* is closely similar to the modern narrow-leafed cottonwood, *P. angustifolia* James. This common Rocky Mountain species has a scattered westward distribution into Nevada and also has a relict occurrence in southern California.[1] Its modern habitats range from the lower borders of the *Juniperus-Artemisia* community well upward into the *Pinus-Abies* forest.

Populus pliotremuloides Axelrod is represented in the Alturas collection by 6 specimens. All of them are small and are essentially indistinguishable from leaves found on aspen today in the drier parts of its distribution. Leaves observed on *P. tremuloides* Michaux now growing in the juniper-sagebrush country directly northeast of Alturas are similar to the fossils in all details. Aspen leaves of larger size and thinner texture have been recorded in near-by Miocene floras as *P. lindgreni* Knowlton. Since they lived under the relatively humid climate that characterized the northern Great Basin in Middle Tertiary time, they resemble closely leaves of *P. tremuloides* in the more mesic parts of its distribution. The presence of the small-leafed Pliocene aspen at Alturas is a reflection of a change from relatively mild Miocene conditions to cooler, semiarid climate by Alturas time.

The paleobotanist regularly encounters difficulty when he attempts to distinguish various fossil willows, or tries to compare them with any one living species of the genus. Not only has there been an overmultiplication of fossil species, but many modern species seem to be ill defined varieties. This large number of modern forms presumably is a result of the diverse environments to which a plastic genus was able to adjust itself in the later Cenozoic. The paleobotanist probably can overcome many of the difficulties accompanying specific determination if he points out resemblances between his material and modern species complexes, and recognizes the potential variation in such groups. Only if similarities between modern and fossil species of willow amount to essential identity does it seem wise to indicate relationship to any one living species.

A study of the Alturas specimens leads to the belief that there are three well defined species in the flora. *Salix truckeana* Chaney is represented in the collection by a specimen that is exactly like leaf impressions in the Lower Pliocene Verdi flora of western Nevada and in the Lower Pliocene Dalles flora of northern Oregon. *Salix truckeana* belongs to the black willow (*S. nigra*) group, and especially resembles leaves of the modern *S. gooddingii* Ball. This willow is distributed through the Upper Sonoran and Lower Transition zones in central California, reappears in southern Arizona, and thence extends southward into Mexico. Among the various plant communities with which it comes into contact may be mentioned the yellow pine and digger pine forests, woodland-chaparral, savanna, and desert.

Salix vanorensis Axelrod is essentially like leaves formed by the modern *S. caudata* (Nuttall) Heller. This species occurs today near the fossil locality,

[1] This has been recorded in various manuals as *Populus trichocarpa* var. *ingrata* Jepson.

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and ranges northward through Canada and eastward into the Rocky Mountains. Over this region it may be found with such diverse communities as montane conifer forest, pinyon-juniper woodland, and Great Basin desert. *Salix vanorensis* has been recorded elsewhere in the transitional Mio-Pliocene Lower Idaho flora and in the Middle Pliocene Deschutes. As discussed in greater detail in the systematic part of this paper, *S. vanorensis* may be a small-leafed segregate of the Miocene *S. hesperia* (Knowlton) Condit.

Salix wildcatensis Axelrod is represented in the collections by 2 leaves which are similar to those of the modern *S. lasiolepis* Bentham. This is a common willow in California, ranging from the redwood and Sierra-Cascade forests in the northern part of the state, southward through the woodland-chaparral country, and into the desert in southern California. It survives also in the Alturas region, where it forms thickets in the juniper-sagebrush country and in the Transition forest. Common in the Pliocene floras of California, and known also from the Pliocene of Oregon, *S. wildcatensis* appears first in the Middle Miocene of southeastern California.

Ulmus moragensis is a small-leafed elm that is known now only from the Alturas and the Middle Pliocene Petaluma and Lafayette Dam floras of west-central California. This species is considerably smaller than *U. speciosa* Newberry of the Upper Oligocene and Miocene, and is smaller also than *U. californica* Lesquereux of the transitional Mio-Pliocene and Lower Pliocene floras of California and Oregon. The paleoecological significance of the different *americana* types of elm in the western United States has been discussed elsewhere by Chaney in this volume (pp. 15–17). He points out that specimens of *U. speciosa* are essentially like those found today on *U. americana* Linnaeus in the more mesic parts of its distribution in the eastern United States. By the early Pliocene there is definite evidence of a smaller-leafed elm of the *americana* type in the fossil record in regions previously occupied by *U. speciosa*. But this species, *U. californica* Lesquereux, resembles more nearly the leaves produced by *U. americana* in the western parts of its distribution in Nebraska, Kansas, and Oklahoma, where it has a strictly flood-plain occurrence in a semiarid climate. Besides being smaller, leaves of *U. californica* also differ from *U. speciosa* in having an average length-width ratio of approximately 2:1 rather than 3:1, and a greater proportion are symmetrical. The change from the larger-leafed *U. speciosa* of the Upper Oligocene and Miocene, which inhabited valley bottoms and upland slopes, to the smaller-leafed *U. californica* of the later Tertiary, with its flood-plain and valley-bottom occurrence under semiarid climate, has been interpreted as a reflection of a change from relatively humid and mild conditions to a more continental type of climate later in the Tertiary.

It is not possible to determine certainly from the material at hand that *U. moragensis* represents the end point in leaf reduction of an *americana* type of elm in response to increased aridity in the western United States following the early Pliocene. None of the specimens reveals sufficient marginal characters to permit such a conclusion. These leaves are like those found on *U. americana*

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in the drier western parts of its distribution, but they are similar also to those of the living *U. pumila* Linnaeus of eastern Asia. The fact, however, that *U. moragensis* occurs in Middle Pliocene floras in areas occupied by the larger-leafed *U. californica* in the Lower Pliocene is strongly suggestive of its derivation from that species. Should further collections show that its affinity lies in this direction, it would be interpreted as a member of the East American Element which became extinct in the later Pliocene. Otherwise, its nearest relative is *U. pumila* of China, and it is a member of the East Asian Element.

From the preceding considerations it is amply clear that the Alturas elm must have lived under conditions like those now found on the western borders of *U. americana* distribution in the High Plains, or where *U. pumila* approaches semiarid regions in the interior of China. In both areas it has a strictly riparian occurrence in regions of low rainfall. The Asiatic elm lives under drier conditions than the American species, and extends along watercourses out into the desert (Chaney, 1935*a*).

In a preceding section of this chapter it has been suggested that the sediments containing the Alturas flora were laid down in a broad river valley occupied by shallow lakes and ponds. It has also been pointed out that the ecological distribution of modern equivalent Alturas species ranges from Transition forest through semiarid woodland and into arid open country where forest and woodland are limited largely to upland slopes away from sites of plant deposition. In order to determine which of these modern habitats represents most closely the conditions of Alturas time, it is now necessary to consider the character of the flora.

The dominant Alturas species, *Populus alexanderi,* provides important evidence with respect to the ecological position of the flora. The modern equivalent of *P. alexanderi, P. trichocarpa,* is a common species along streams in northeastern California and adjacent Nevada and Oregon. In this area it is to be found in forests or in semiarid open country below the forest zone, where trees are confined to stream banks. The first of these habitats may readily be seen along the highway which follows the valley of Rush Creek 12 miles southwest of the fossil locality (pl. 47, fig. 1). Here at an elevation of from 4800 to 5000 feet black cottonwood forms dense stands along the broad creek bottom. Among its associates are the following:

Amelanchier alnifolia Nuttall
Cornus glabrata Bentham
Crataegus douglasii Lindley
Malus rivularis (Douglas) Roemer
Prunus demissa (Nuttall) Walpers
Rosa pisocarpa Gray
Salix caudata (Nuttall) Heller
Salix lasiolepis Bentham
Salix lemmonii Bebb

Populus tremuloides Michaux is represented also in this riparian community, but is not so numerous as the black cottonwood. *Pinus ponderosa* Douglas and *Quercus kelloggii* Newberry are the forest dominants, and with a rise of 500 feet *Abies concolor* (Gordon) Parry is a frequent associate. The drier and

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more exposed slopes in this area support a juniper-sagebrush community characterized by:

Artemisia tridentata Nuttall
Cercocarpus ledifolius Nuttall
Juniperus occidentalis Hooker
Purshia tridentata DeCandolle
Wyethia mollis Gray

This association commonly extends to the edges of the creek along the exposed ridges and flats, and from such areas may contribute occasional leaves and twigs to the stream.

The absence of typical forest and woodland trees or shrubs from the Alturas record strongly suggests that the flora lived in semiarid open country below these vegetation zones. At the present time, needles, cone scales, leaves, and twigs of the yellow pine and juniper-sagebrush communities are common in stream deposits in those associations. They also are frequently carried out into semiarid areas, where they mingle with leaves of strictly riparian trees and shrubs in quiet pools. Had members of forest or woodland communities lived near Rattlesnake Butte at the time of leaf deposition, one might expect them to have a limited occurrence in the record. Their absence from the Alturas flora is thus interpreted as indicating that they did not survive as important communities over the lowlands in Alturas time. Since remains of forest and woodland vegetation dominate all known Miocene and Lower Pliocene floras over the present desert and semidesert regions from northern Oregon southward into central Nevada, it would seem to be a foregone conclusion that they would be present had these types lived near sites of deposition.

It is thus believed that the modern habitat of black cottonwood in northeastern California and adjacent areas, along the flood plains of streams and rivers below the forested zone, more nearly represents the conditions of Alturas time. A habitat of this general type in near-by Oregon is shown in plate 47, figure 2. In such areas black cottonwood is found in open country surrounded largely by Great Basin sagebrush and grassland. Its associates along stream banks include various species of *Amelanchier, Betula, Prunus, Rosa, Salix,* and *Sambucus.* Aspen occurs also with black cottonwood in this open country, but here it forms a less prominent member of the riparian community. In areas where the two are associated, black cottonwood occurs typically at levels below aspen. It is significant in this connection that the leaves of *Populus alexanderi* outnumber those of *P. pliotremuloides* by more than ten to one in the Alturas collections. This dominance of black cottonwood over aspen suggests that the lower borders of black cottonwood distribution in open country below the forest zone probably resemble the Alturas habitat. Although it must be admitted that a larger Alturas collection might show that woodland or forest vegetation occurred in this area, it seems highly unlikely that its distribution was other than one of isolated colonies on cooler bordering slopes.

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For these reasons, climatic conditions of Alturas time are considered to resemble most nearly those found today in semiarid open country below forest and woodland. The average annual rainfall at Alturas, 10 miles east of the fossil locality and at the same elevation, is now 12.65 inches, as based on a 16-year record. This area is on the lower edge of juniper-sagebrush country. The more typical associates of this community, which is dominated by *Artemisia tridentata* and *Juniperus occidentalis,* include *Amelanchier alnifolia, Chrysothamnus nauseosus, Peraphyllum ramosissimum, Purshia tridentata,* and *Ribes inerme.* The borders of ponds and streams in the Pit River valley within a short distance of the fossil locality support colonies of *Typha latifolia, Populus tremuloides, Prunus demissa,* and *Nymphaea polysepala,* as well as of *Rosa* (*R. pisocarpa, R. ultramontana*) and *Salix* (*S. caudata, S. lasiolepis*). In the hills directly southwest of Rattlesnake Butte, at an elevation fully 500 feet above the floor of the valley, there is a typical Transition forest of *Abies concolor, Pinus ponderosa,* and their common associates. It seems evident that if rainfall during Alturas time had greatly exceeded 15 inches, one might expect a record of woodland vegetation and occasional indications of a near-by Transition forest, for they occur today in stream deposits along the Pit River valley. Their absence from the Alturas record is interpreted as indicating that precipitation in this area probably averaged 12 inches yearly and did not exceed 15.

Such a figure implies that there has been but little change in total yearly rainfall in this area since the Alturas stage, a conclusion at variance with the well established trend toward lowered rainfall in this region during the successive stages of the later Tertiary. Of the several ways in which this discrepancy might be explained, the following seem more important:

1. The Alturas region may have been at a lower elevation during the later Tertiary than it is today. If it could be demonstrated that the Modoc plateau was from 1000 to 2000 feet lower during the Alturas stage, a comparison of rainfall at these lower levels today with the suggested Alturas precipitation would reveal a rainfall reduction. But on geologic grounds it is not certain that the Alturas area had an elevation in the Pliocene greatly different from that of today. This interior area, which is a part of the Great Basin province, is a relatively flat-lying plateau with an average elevation of from 4500 to 5000 feet. It shows but little evidence of late Tertiary geologic disturbance except block faulting. The most widespread rocks in northeastern California are the Warner and related basalts, which are essentially horizontal except where disturbed by comparatively recent faulting. The Warner basalt rests conformably on the Alturas formation, and also covers the Upper Cedarville in many places, with concordance. There is evidence of only local disturbance in northeastern California in the interval between Upper Cedarville (Middle to Upper Miocene) and Warner basalt time (late Cenozoic). Only if it could be demonstrated that there has been general epeiric uplift in northeastern California since Alturas time would there be evidence for asserting that the Alturas site of deposition was lower than it is today. The writer is not aware of any incontrovertible evidence leading to such a conclusion, unless it lies in the widely held belief

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that the whole western part of the continent has been a rising land area throughout and since later Tertiary time. But even so there is no way to estimate closely the amount of uplift in northeastern California following Alturas time.

2. The later Tertiary floras showing a progressive trend toward aridity are situated on the leeward slopes of mountains which have been elevated considerably since the later Pliocene. Uplift of the Cascades on the windward side of the Deschutes, and of the Sierra Nevada to the west of the Upper Truckee, explains the continued trend toward lowered rainfall in those areas following the Middle Pliocene. Both floras occur in a region now steppe and desert which came into existence only in the latest Cenozoic as the rising mountains intercepted rain-bearing winds. It is thus of some importance that no high mountain range was elevated directly west of Alturas in the later Cenozoic.

3. There are other Pliocene floras in the western United States besides the Alturas that show but little change between that period and the present in the amount of rainfall at the site of deposition. The Oakdale flora from the central Sierran foothills lived under an annual rainfall hardly 5 inches higher than is found in that area today. The Mulholland and Petaluma floras of west-central California reflect a slightly drier climate than is now found in those areas. By contrast, rainfall during both the Lower and the Upper Pliocene was heavier in central California than that now occurring there. It thus appears that in many areas precipitation today would be essentially like that of the Middle Pliocene except that it has been reduced by the elevation of barriers to the west.

It is therefore believed that there are no real discrepancies in our interpretation of Alturas climate. The main factor accounting for a relatively stable total precipitation here may be that no mountain barrier comparable with the Sierra Nevada or Cascades was raised to the west of the Alturas area following deposition of the flora. On the other hand, if it can be demonstrated that the flora has been elevated to its present position since Alturas time from an altitude 1000 feet or more lower, a reduction of perhaps 5 inches in rainfall has taken place since the time of floral deposition. Although geological evidence for uplift of the Modoc plateau is not conclusive, a similar total rainfall for this area in Alturas time and today is not incompatible with evidence for the general trend toward aridity in the western United States. There are other Pliocene floras in California showing a similar relation.

In any event, it is certain that climatic changes more fundamental to altered plant distribution have taken place in northeastern California since Alturas time than a slight lowering of rainfall, which may readily be compensated for in semiarid regions by a rise of a few hundred feet in elevation. These changes have involved the lowering of winter temperature and the gradual disappearance of effective summer rains. Some of the Alturas species providing data with respect to these climatic features may now be considered. If one compares the Alturas leaves of *Populus alexanderi* with those of the modern *P. trichocarpa* living near the fossil locality, a significant fact immediately appears. The nearest black cottonwood trees observed were found in the yellow pine forest along Rush Creek 12 miles southwest of Rattlesnake Butte, where they are separated

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from the fossil locality by a high ridge. Here the leaves of *trichocarpa* are two to three times as large as the Alturas fossils. This same relation has been noted also in the Pliocene Verdi flora near Reno, Nevada. Over 1000 specimens of *P. alexanderi* have been examined in the Verdi collections, and all of them are small. The modern *trichocarpa* growing along the Truckee River within 100 yards of the fossil locality has leaves that are typically from two to four times as large as those of the Verdi *P. alexanderi*. The Deschutes florule of eastern Oregon likewise has leaves of *P. alexanderi* that are relatively small and of thick texture (Chaney, 1938*a*). Comparison of the Deschutes specimens with leaves from *trichocarpa* in the near-by mountains of eastern Oregon also illustrates the fact that the Pliocene species is characterized by leaves that are definitely smaller than those of its modern relative in that area.

It is believed that in the case of *P. alexanderi* in the Alturas flora, as well as in the Verdi and Deschutes assemblages, we are dealing with an ecotype of *trichocarpa* which has no modern counterpart in the western interior (Axelrod, 1941). Specimens of *P. alexanderi* from all these localities resemble more nearly the leaves of black cottonwood at lower levels in the south Coast Ranges and in southern California. The modern form of *trichocarpa* found today in western Nevada, northeastern California, and eastern Oregon tolerates conditions definitely colder than those implied by its smaller-leafed Pliocene relative. Such a relation assumes considerable importance in the case of floras with a limited number of plants, like the Alturas or Deschutes. As will be pointed out in a later section of this chapter, this small-leafed ecotype of *trichocarpa* also has important age implications in these floras.

This suggestion of milder winters in northeastern California during Alturas time than today is consistent with the present distribution of one of the willows having an equivalent in the flora. *Salix truckeana* Chaney resembles the modern *S. gooddingii,* which occurs in central and southern California, as well as in southern Arizona and Mexico. All these areas have warmer winters than Alturas does today. Supplementary evidence for milder winters in this area during the Pliocene is provided by the character of the later Tertiary floras in near-by regions, as discussed in this volume and elsewhere.

The occurrence of summer rainfall during Alturas time is suggested by the presence of *Ulmus moragensis* and *Populus payettensis* in the flora. *Ulmus* survives today only in areas with summer precipitation in eastern North America and eastern Asia. The narrow-leafed cottonwood, *P. angustifolia,* is typical of the Rocky Mountain area where there are regular summer showers. Additional evidence for summer rains in Pliocene time has been summarized previously (Axelrod, 1940*a,* pp. 166–168), as well as in chapter 8 of this volume. It is perhaps sufficient to recall here that the regular presence of members of the East American and East Asian Elements, as well as of the Madro-Tertiary Flora with surviving equivalents in the southwestern United States and Mexico, in the Pliocene floras of California, Nevada, and Oregon suggests that summer rains occurred in this epoch. Summer rains were less than those of the Miocene, and their general effectiveness on plant distribution was reduced first at the

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interior, owing to a higher evaporation rate there than in coastal and maritime areas.

The evidence regarding the physical conditions near Rattlesnake Butte during the deposition of the Alturas formation may be summarized as follows:

1. The character of the Alturas sediments and the mode of leaf accumulation suggest plant deposition in the shallow lakes or ponds of a broad river valley not greatly unlike the Pit River valley near the fossil locality today.

2. The composition of the flora, which is strictly riparian and dominated by cottonwoods and willows, suggests semiarid open country in which forest and woodland were restricted to higher elevations and to more distant slopes. Present stream-border vegetation below the zone of forest and woodland country, resembling the Alturas, lives under an annual rainfall of from 12 to 15 inches, which is considered to represent rather closely the average during Alturas time.

3. Certain species in the flora suggest that (*a*) precipitation occurred as summer showers and winter rains, and that (*b*) winters were milder than those now occurring in northeastern California.

Climatic changes fundamental to altered plant distribution have involved a modification of these latter factors. Although summer showers for the months of May through September now amount to about 20 per cent of the yearly total, they are largely lost through rapid evaporation. These showers are ineffective as compared with those of Alturas time, which were sufficient to support an elm and a cottonwood now represented by related species in areas with summer showers. In response to the trend toward lowered winter temperatures in this area, resulting in a shorter growing season, a small-leafed ecotype of black cottonwood (*Populus alexanderi*) was eliminated from the province. A modern willow with a close equivalent in the flora likewise now occurs in central California and adjacent regions where winters are warmer than in northeastern California. Only the hardier Alturas species of aspen and willow have survived in closely similar form along streams in this region.

Age of the Flora

Two general lines of paleobotanical evidence will be used in determining the age of the Alturas flora. These will involve, first, the stratigraphic distribution of its species in other fossil floras in the western United States, and, second, the climatic and floral character of the Alturas as compared with floras in the adjacent Great Basin province, and in west-central Nevada. Supplementary evidence for its age is provided by the associated Alturas vertebrate fauna.

All Alturas species are represented by identical or closely related plants in Miocene or Pliocene floras in the western United States. The more important localities where these species occur are listed in table 24, where an x signifies the presence of the Alturas species and an o denotes a closely related and presumably ancestral form. It is amply clear from this table that the Alturas species occur with greatest frequency in Pliocene floras, and that plants ancestral to them are largely in the Miocene. The Alturas species *Populus alexanderi, P. pliotremuloides,* and *Salix vanorensis* are represented in Miocene floras at

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TABLE 24

STRATIGRAPHIC DISTRIBUTION OF ALTURAS SPECIES

Species	Miocene: Middle and Upper: Tehachapi	Trout Creek	Payette	Thorn Creek	Upper Cedarville	Transitional: Lower Idaho	Remington Hill	Table Mountain	Pliocene: Lower: Esmeralda	Verdi	Alvord Creek	Dalles	Black Hawk Ranch	Middle: Lafayette Dam	Mulholland	Deschutes	Petaluma	Oakdale	Upper: Sonoma
Populus alexanderi	x	..	o	o	o	o	x	..	x	x	..	..	..	x	x	x	x	x	x
Populus payettensis	..	..	x	x	..	..	..	..	..	x	x	..	..	..	..	..	..	..	....
Populus pliotremuloides	x	o	o	o	..	..	x	..	x	x	x	..	..	..	..	x	..	x	x
Salix truckeana	..	..	..	..	..	..	..	..	..	x	..	x	..	..	..	..	..	..	....
Salix vanorensis	..	..	o	o	o	x	o	..	..	..	..	o	o	..	o	x	o	..	....
Salix wildcatensis	x	..	..	..	..	..	..	..	..	..	..	..	..	..	x	..	x	x	x
Ulmus moragensis	..	..	..	..	..	o	o	o	..	..	..	o	o	x	..	..	x	..	....
Identical species	3	0	1	1	0	1	2	0	2	4	2	1	0	2	2	3	3	3	3
Related species	0	1	3	3	2	2	2	1	0	0	0	2	2	0	1	0	1	0	0
Identical species in stage			4				3				4					5			3
Related species in stage			1				1				2					0			0
Identical species in epoch					5								7						
Related species in epoch					1								0						

x = identical species; o = related species.

the latitude of Alturas by *Populus eotremuloides, P. lindgreni,* and *Salix hesperia,* respectively. As was pointed out in the discussion of the composition of the flora, the Alturas species in all cases have leaves of smaller size and thicker texture than their Miocene relatives. Their development in response to increased aridity in this region following the Miocene clearly denotes a Pliocene age for the flora. One must not be confused by the occurrence of such species as *Populus alexanderi* and *P. pliotremuloides* in the Middle Miocene Tehachapi flora of southeastern California, for semiarid conditions had already developed there by that stage. It cannot be emphasized too strongly that semiarid conditions suited to the evolution of small-leafed derivative species appear at different times in the various paleobotanical provinces, depending on latitude and position with respect to the ocean, and that these small-leafed species occur in the northern Great Basin only in post-Miocene time.

Although table 24 unquestionably demonstrates the Pliocene age of the Alturas, assignment to any one stage of the epoch is difficult from these data. It may be noted, however, that *Ulmus moragensis* is smaller than *U. californica* of the

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Lower Pliocene and transitional Mio-Pliocene floras. The fact that it is known to appear only in post-Lower Pliocene time in regions previously occupied by *U. californica* suggests a post-Lower Pliocene age for the flora.

In the case of Pliocene floras, the usual method of studying the stratigraphic range of the species is inadequate for close age assignment. This is due to the fact that Pliocene floras vary locally in response to physical conditions which are modified according to geographic location with respect to elevation, mountains, and the ocean. This feature alone has made it difficult to determine the age of a Pliocene flora from specific comparison with other floras. Such a procedure nearly always resolves itself into trying to prove the contemporaneity of such dissimilar types of vegetation as redwood forest, woodland, and flood plain. More recent studies of Pliocene floras have shown that owing to rapid changes in environmental conditions in this epoch, there is a continuous succession of vegetation types in each province (Axelrod, 1938, 1940*b;* chap. 8 above). For these reasons, a precise age assignment can be given to a Pliocene flora only if it is evaluated from the standpoint of its position in an established, or at least reasonably inferred, climatic and floral sequence in the immediate region (chap. 8). In the case of the Alturas, comparison must be made with floras in the adjacent northern Great Basin. A comparison with floras in central Nevada, west-central California, or northern Oregon will only serve to emphasize the diversity of Pliocene environments, rather than indicating the age of the Alturas. If, however, the age of the Alturas can be established independently, and if it can then be shown that contemporaneous vegetation in other provinces reflects a similar climate as based on a reasonably complete Pliocene sequence, this should then provide corroborative evidence with respect to its age.

Previously described floras nearest to the Alturas which may be used in evaluating its age include the Middle to Upper Miocene Upper Cedarville flora of the immediate region (LaMotte, 1936), the transitional Mio-Pliocene Lower Idaho flora 290 miles northeast (Dorf, 1936; Smith, 1938*a*), the Lower Pliocene Alvord Creek flora of southeastern Oregon 130 miles northeast (chap. 9 above), and the Middle Pliocene Deschutes flora 240 miles north (Chaney, 1938*a*). The succession of vegetation and climate indicated by these floras is so well understood that only a summary of their physical relationships need be presented here. Changing physical conditions in this general region from Upper Cedarville to Deschutes time may be tabulated as shown in table 25.

The floral and climatic succession shown by these floras presents conclusive evidence for asserting that there has been a general trend from (*a*) moist, temperate Miocene climate, with forests dominant in lowland areas near sites of plant deposition, to (*b*) cool, semiarid climate in the Pliocene, with hardier trees and shrubs surviving along stream banks in the semiarid open country below the zone of forest vegetation. This change in environment has been correlated with the rising Cascade mountain barrier at the west, modifying physical conditions in its lee (Chaney, 1936*b*, 1938*b*, 1938*c;* chap. 11 below).

When the Alturas vegetation and climate are compared with this succession, it is at once apparent that the flora is Pliocene in age, and that it represents

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TABLE 25

FLORAL AND CLIMATIC SUCCESSION IN THE NORTHERN GREAT BASIN

Flora	*Floral features*	*Climate*
Deschutes (Middle Pliocene)	West American Element predominant: *Acer*, *Populus*, *Prunus*, *Salix*.	Cool semiarid; rainfall 15 inches yearly; some summer showers; summer and winter extremes like those of Alturas stage.
Alturas (Middle Pliocene)	West American Element predominant: *Populus*, *Salix*. East American or East Asian Element very rare and represented by derivative species: *Ulmus*.	Semiarid; rainfall 12 to 15 inches yearly; winter rains and some summer showers; higher summer and lower winter temperatures than earlier in epoch.
Alvord Creek (Lower Pliocene)	West American Element dominant: *Abies*, *Acer*, *Amelanchier*, *Picea*, *Pinus*, *Populus*, *Pseudotsuga*, *Rosa*, *Sorbus*. Leaves of *Acer*, *Amelanchier*, *Populus*, and *Rosa* definitely smaller than those of related Miocene species. Southwest American Element prominent: *Amorpha*, *Arbutus*, *Ceanothus*, *Cercocarpus*, *Juniperus*. East American and East Asian Elements with relict occurrences: *Abies*, *Carpinus*, *Prunus*, *Rhus*.	Semiarid; rainfall 20 to 30 inches yearly; precipitation biseasonal; higher summer and lower winter temperatures than earlier in the Tertiary.
Lower Idaho (Transitional Mio-Pliocene)	West American Element dominant: *Abies*, *Acer*, *Alnus*, *Betula*, *Castanopsis*, *Fraxinus*, *Pinus*, *Prunus*, *Quercus*, *Salix*, *Sequoia*, *Thuja*. East American and East Asian Elements holding a less prominent place here than earlier in the epoch: *Acer*, *Cercidiphyllum*, *Juglans*, *Ostrya*, *Platanus*, *Ptelea*, *Quercus*, *Trapa*, *Ulmus*. Southwest American Element not uncommon: *Arbutus*, *Juniperus*, *Pinus*, *Quercus*. Caribbean Element not uncommon: *Cedrela*, *Celastrus*.	Temperate with a semiarid aspect; annual rainfall 25 to 35 inches,* distributed in summer and winter months but not so evenly as during the Miocene; summers hotter and winters colder than in the Miocene.
Upper Cedarville (Middle to Upper Miocene)	East American and East Asian Elements characteristic: *Carya*, *Cebatha*, *Cercidiphyllum*, *Fagus*, *Ginkgo*, *Nyssa*, *Platanus*, *Populus*, *Tilia*, *Ulmus*. West American Element common: *Abies*, *Acer*, *Alnus*, *Fraxinus*, *Pinus*, *Populus*, *Rosa*, *Salix*, *Sequoia*. Caribbean Element common: *Cedrela*, *Oreopanax*.	Temperate; rainfall distributed rather evenly throughout the year; totaling 35 to 45 inches.*

*In the writer's opinion, the rainfall estimates given by Dorf (1936) and LaMotte (1936) are too low for these floras.

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Middle or Upper Pliocene time. The reasons leading to this conclusion may be summarized as follows:

1. A rainfall figure of 12 to 15 inches for the Alturas, as compared with 35 inches and more for the Middle to Upper Miocene, 25 to 35 inches in the Mio-Pliocene transition, and 20 to 30 inches in the Lower Pliocene, represents a continued lowering sufficient to suggest its post-Lower Pliocene age.

2. There is a gradual reduction in members of the East American and East Asian Elements from Upper Cedarville time up through the sequence. During the Mio-Pliocene transition they still have a large generic representation but form less prominent elements from a quantitative standpoint than in the Miocene. Lower Pliocene records of these elements are in all cases relicts which were surviving in favorable sites. A small-leafed elm, *Ulmus moragensis,* is the only record of this group at Alturas. This species is considerably smaller than the Miocene *U. speciosa* of the immediate region, and is smaller also than *U. californica* of the Lower Pliocene floras immediately to the north and south. *Ulmus moragensis* is now known only from floras of post-Lower Pliocene age in regions previously occupied by *U. californica;* this implies a post-Lower Pliocene age for the flora. The absence of other members of the East American and East Asian Elements from the flora provides corroborative evidence for such an assignment.

3. Members of the West American Element gradually increase as the climate becomes cooler in the later Miocene and early Pliocene, and they predominate in the Lower Pliocene. But two of the important components of this element, the Redwood and North-coast coniferous, which have a major place in Miocene floras and a subordinate position in the Mio-Pliocene transition, are unknown in the Lower Pliocene of the northern Great Basin. They presumably disappeared as the more sensitive members of the East American and East Asian Elements became extinct. Their reduction at the interior implies a more rigorous climate and a lower total rainfall.

The dominance of members of the Sierra-Cascade, Rocky Mountain, and Border-redwood Components in the Lower Pliocene indicates a more continental type of climate than earlier in the series. Only the hardier species of willow (*Salix*), cottonwood (*Populus*), and aspen (*Populus*) of these components survived over the lowland depositional basins at the interior in Alturas time. The typical Transition forest members of these components seem to have been limited to moister upland slopes away from sites of deposition at this later date, and therefore did not become a part of the fossil record. This change from forest to riparian vegetation seems to establish the post-Lower Pliocene age of the Alturas.

4. The Southwest American Element appears as an important group in the northern Great Basin in the Mio-Pliocene transition, and increases in abundance in the Lower Pliocene as conditions become drier over the lowlands. If woodland or chaparral species occurred in the Alturas region, they had a highly restricted distribution and did not enter the record. The absence of members of this element representing the woodland or chaparral of central California or

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the southwestern United States implies a post-Lower Pliocene age for the flora, for they were common here during that stage.

It is clear without laboring the point that the Alturas more closely resembles the Deschutes than any other flora in this region. Like the Alturas, the Deschutes points to a climate sufficiently arid to restrict forest cover, which had been dominant near sites of deposition in the Lower Pliocene, into moister upland habitats away from basins of plant accumulation. Both floras are made up of hardy derivative Miocene trees and shrubs which survived only along stream banks in semiarid open country below the zone of forest vegetation. These floras have three species in common, *Populus alexanderi, P. pliotremuloides,* and *Salix vanorensis.* The Deschutes seems to be slightly more mesic than the Alturas on the basis of the dominance of aspen there. Such differences, however, cannot be considered as important from a stratigraphic standpoint, for they are readily ascribable to local habitats.

This comparison with floras in the adjacent region gives ample reason for concluding that the Alturas is younger than Lower Pliocene. But it is difficult to determine from these floras whether the Alturas belongs to the middle or upper part of that epoch. Evidence for assigning the flora to the Middle rather than to the Upper Pliocene is provided by the paleoecological implications of *Populus alexanderi,* the dominant species of the flora. In the discussion of the physical conditions, it has been pointed out that the Alturas leaves of *P. alexanderi* are most nearly like those now found on *P. trichocarpa* in the drier and warmer parts of its distribution, in the south Coast Ranges and in southern California. By contrast, the leaves of *trichocarpa* in the vicinity of Alturas are from two to three times as large as the fossils, have a thinner texture, and often are serrate rather than entire-margined. The small-leafed Pliocene species is considered to reflect winters considerably milder than those in the Alturas region today. Since the climate was becoming cooler in the later part of the epoch, if the flora were Upper Pliocene in age one might expect the Alturas leaves of black cottonwood to be more nearly like those found on *trichocarpa* in that region today. On this ground it may readily be argued that the flora is more probably Middle than Upper Pliocene in age.

If the Alturas actually reflects a warmer climate than may have prevailed here in the Upper Pliocene, corroborative evidence should be found in the Middle and Upper Pliocene floras in near-by regions. It is in this connection that the later Pliocene floral sequence in central California is important to the present discussion. The floras of this region, which have been reviewed in chapter 8 of this volume, show conclusively that the Middle Pliocene was characterized by conditions definitely warmer than prevail in that area today. Such floras as the Mulholland and Petaluma of west-central California clearly suggest a warmer and drier climate than is now found in those regions. In the Upper Pliocene, as indicated by the Santa Clara and Sonoma floras, conditions became cooler and more moist.

From these data there seems to be evidence for a general contemporaneity of moderately warm, semiarid climate in the northern Great Basin and in cen-

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tral California in Middle Pliocene time. It must be emphasized that this suggested age agreement between the Alturas and the Middle Pliocene floras of central California has not been indicated by a large number of Alturas species in these floras. There is as little in common between the Middle Pliocene floras of central California and the Alturas as between the types of vegetation now living in these two areas. On the contrary, the age agreement has been determined on the basis of a known climatic trend progressively modifying different vegetation types to the same stage of floral evolution. Only by understanding the succession of vegetation in each area through the Pliocene is it possible to show that dissimilar vegetations may be of essentially the same age.

Supplementary floral evidence for the Middle Pliocene age of the Alturas is provided by current studies of floras from west-central Nevada whose ages include late Upper Miocene and Lower Pliocene. In the late Miocene, judging from the Coal Valley and Lower Truckee floras, an oak-juniper woodland dominated near sites of deposition, with members of a montane forest of *Abies, Castanopsis, Mahonia, Populus,* and their associates near at hand. Annual rainfall at this time is considered to have ranged from 20 to 25 inches. By the Lower Pliocene, with a decrease of from 5 to 7 inches in yearly precipitation as gauged from the Esmeralda flora (Axelrod, 1940*a*), oak-juniper woodland still dominated over the lowland sites of deposition; but members of the montane forest were essentially absent and there was an increase in semiarid shrubs. It is evident that this change in the character of the woodland in the west-central Great Basin from late Miocene to Lower Pliocene time is closely similar to that which took place in the northern Great Basin during the same interval, although in each case the flora at the south is more arid. One might expect that only hardier riparian trees and shrubs would have survived along watercourses over the lowlands of west-central Nevada by the Middle Pliocene. In other words, it is believed that the recognition of a strictly riparian distribution for trees in the region now desert and semidesert by the Middle Pliocene may be of considerable value for north-south correlation in these provinces in the lee of the Cascade-Sierran barrier. Since the vegetation of southern Oregon and central Nevada was largely distinct in late Miocene and Lower Pliocene times, specific correlation between floras of these provinces would hardly be expected later in the Pliocene. Only in the fact that the climate was sufficiently arid to restrict trees to stream banks would there be any suggestion of essential age agreement. Upper Pliocene floras are not known from the Great Basin, but judging from the known floral succession one might expect them to resemble stream-bank communities near at hand. Their post-Middle Pliocene age would presumably be indicated by the absence of (*a*) members of the Southwest American Element now found in central and southern California or the southwestern United States, (*b*) members of the East Asian and East American Elements, as exemplified by *Ulmus* at Alturas, and (*c*) perhaps also, species of the West American Element whose equivalents now live in regions having milder winters than those of the Great Basin, such as *Populus alexanderi* and *Salix truckeana* of the Alturas.

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Additional paleontological evidence for the age of the Alturas formation is presented by the Alturas fauna, which comes from several localities near Rattlesnake Butte (Stirton, *in* LaMotte, 1936, p. 105). The fauna is small and most of the material is so fragmentary that reference can be made only to families or to genera. The assemblage includes representatives of *Alticamelus* sp., *Vulpes* sp., and *Neohipparion* sp., in addition to Camelidae, Carnivora, Mastodontinae, Rhinocerotidae, and Tayassuidae. In commenting on these genera, Stirton points out that *Neohipparion* sp. resembles material from the Thousand Creek and Rattlesnake faunas, which are of Middle Pliocene age. *Vulpes* sp. is like specimens from the Upper Miocene Snake Creek, but is somewhat larger. *Alticamelus* sp. ranges from the Upper Miocene through the Lower Pliocene, and has not certainly been recorded from any Middle Pliocene fauna.

The Alturas fauna has been assigned to the late Lower Pliocene, but it has been pointed out that accurate age determination of the formation cannot be made from this fragmentary material. It seems clear that if the flora is Lower Pliocene it can belong only to the latest part of that stage, in which case there is close agreement with vertebrate evidence. On the basis of the floral evidence now at hand it seems probable that more adequate vertebrate material might show the Alturas fauna to be Middle Pliocene in age.

Summarizing the evidence for the age of the Alturas flora, the following points may be listed:

1. The composition of the flora and its physical conditions, when compared with those of a succession of floras in the adjacent northern Great Basin, suggest a Middle Pliocene age.

2. A similar but less complete succession in the west-central Great Basin apparently reaches a comparable stage of floral evolution during the Middle Pliocene.

3. The Alturas vertebrate fauna is represented by fragmentary material tentatively referred to the late Lower Pliocene. If the flora is Lower Pliocene, it can belong only to the latest part of that stage, but present evidence more strongly suggests a Middle Pliocene age assignment.

Summary

The Alturas flora of 7 species from the Great Basin province in northeastern California is a flood-plain assemblage of aspen, cottonwoods, elm, and willows; these are hardy derivatives from floras of the Miocene and Lower Pliocene. The flora resembles modern riparian communities beyond the borders of forested country in North America and eastern Asia, where rainfall is from 12 to 15 inches yearly.

The Middle Pliocene age of the flora is indicated by comparison with sequences of floras in the adjacent and more southerly parts of the Great Basin. Riparian vegetation in regions dominated by forest and woodland in the Lower Pliocene, and now desert or semidesert, is strong evidence for a Middle or Upper Pliocene age; allocation to either stage may be gauged from floral composition.

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SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class ANGIOSPERMAE
Subclass DICOTYLEDONES
Family SALICACEAE

Populus alexanderi Dorf

(Plate 48, figure 4)

Populus alexanderi Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 75–77, pl. 6, figs. 10, 11 (not fig. 9, which is *P. prefremontii* Dorf); pl. 7, figs. 2, 3 (not fig. 1, which is *P. prefremontii*), 1930.

Condit, Carnegie Inst. Wash. Pub. 553, p. 40, 1944 (see synonymy).

One of the specimens figured by Dorf from the Alturas (Dorf, 1930, pl. 6, fig. 10) is near the maximum size for *Populus alexanderi*. It can be distinguished from leaves of *P. eotremuloides* Knowlton of essentially similar size from the Upper Miocene near by (LaMotte, 1936, pl. 5, figs. 7, 9) on the basis of subsidiary teeth rather than moderately strong ones.

An additional Alturas specimen is figured here in order to convey the idea of the relatively small size and oval shape which is typical of the species, as judged from the numerous specimens in the Pliocene collections from California, Nevada, and Oregon at the University of California.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2362; nos. 2363, 2364, 2375; (nos. 328 and 329 are Dorf's types).

Populus payettensis (Knowlton) Axelrod

(Plate 48, figure 3)

Populus payettensis (Knowlton) Axelrod, Carnegie Inst. Wash. Pub. 553, p. 253, 1944 (see synonymy).

Populus payettensis is a slender-leafed cottonwood related to the modern *P. angustifolia* James, which is typical of the Rocky Mountain region. Its nearest occurrences to Alturas are in southwestern Idaho and in central Nevada.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2365; no. 2366.

Populus pliotremuloides Axelrod

(Plate 48, figure 6)

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. 476, III, pp. 169–170, pl. 4, figs. 1–3, 1938.

Populus pliotremuloides had a wide distribution in the western United States in later Tertiary time. Its occurrence with diverse plant associations, ranging from redwood forest to woodland and chaparral, has led to the suggestion that it had several ecotypes which are no longer represented in the modern flora by *P. tremuloides* Michaux (Axelrod, 1941).

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2367; no. 2368.

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Salix truckeana Chaney

Salix truckeana Chaney, Carnegie Inst. Wash. Pub. 553, p. 316, pl. 52, figs. 2–6, 1944.

This species is readily recognized by its linear shape, serrate margin, and fine secondaries which diverge at high angles from the midrib and then loop sharply upward in the outer part of the blade and extend along the margin for a considerable distance. Among living species *Salix gooddingii* Ball, a member of the black willow group, is not greatly different from the fossil.

On the basis of additional material it may be possible to show that *S. truckeana* is a small-leafed derivative of *S. longiacuminata* Knowlton, which is represented in Eocene, Oligocene, and Miocene floras in western North America.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2369.

Salix vanorensis new name

(Plate 48, figures 1, 2)

Salix florissanti Knowlton and Cockerell. Chaney, Carnegie Inst. Wash. Pub. 476, IV, pp. 215–216, pl. 6, fig. 3, 1938 (see synonymy).

Salix coalingensis Dorf (in part), Carnegie Inst. Wash. Pub. 476, II, p. 110, 1936.

The Deschutes leaves identified as *Salix florissanti,* and the Lower Idaho specimen (no. 1174) referred to *S. coalingensis,* are indistinguishable from material in the Alturas flora. These specimens are not properly referable to *S. florissanti* because that species represents *Populus* rather than *Salix,* as may be seen from the character of the marginal teeth and the large petiole. Nor can they be referred to the two willows, *S. wildcatensis* and *S. hesperia,* which were included previously in *S. coalingensis.* For this reason a new name, *vanorensis,* has been chosen for the species; the name has been taken from Vanora Grade, where the Deschutes flora occurs. The figured Deschutes type is described below, with important variations contributed by the Lower Idaho and Alturas material.

Description. Leaves slender, lanceolate; acute to subacuminate above and acute below; larger leaves 7.8 cm. long and 1.5 cm. wide, smaller ones 4.7 cm. long and 1.3 cm. wide; petiole stout, 0.5 to 1.0 cm. long; midrib firm, curved or straight, slender in the upper part of the blade; numerous alternate secondaries and conspicuous intersecondaries diverging from the midrib at 25° to 35°, looping upward symmetrically and following just within the margin for some distance along the blade, subcamptodrome, joining the secondaries above by numerous crossties; tertiary venation coarse and irregular; margin serrate; texture medium to subcoriaceous.

Discussion. Salix vanorensis is similar to the leaves of the modern *S. caudata* (Nuttall) Heller, which ranges from northeastern California into Canada and eastward to the Rocky Mountains. *Salix caudata* is related to *S. lasiandra* Bentham and has been considered by certain authorities to be a variety of that species. The interrelations of the slender-leafed varieties of *lasiandra,* and their similarity to the fossil, suggest the probable origin of the latter species. The large-leafed *S. hesperia,* which has been considered related to *S. lasiandra,* was common in the northern Great Basin and Columbia Plateau in the Miocene. It would appear that *S. vanorensis* may have been differentiated from *S. hesperia* in the later Miocene as that species was restricted coastward to areas of more moderate climate. Its smaller-leafed differentiate, *S. vanorensis,* has persisted at the interior as the closely related *S. caudata.*

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Salix venosiuscula H. V. Smith from Thorn Creek (Smith, 1941, pl. 3, fig. 7) has been compared with *S. fendleriana* Anderson (= *S. caudata*) of the Rocky Mountain region. *Salix venosiuscula,* however, seems to be a small leaf of the Thorn Creek *S. schimperi* Lesquereux (Smith, 1941, pl. 5, fig. 1), which in turn is referable to *S. hesperia.* The leaves of *S. cordata* Muhlenberg, with which the Thorn Creek *S. schimperi* has been compared (Smith, 1941, pl. 5, fig. 2), are wider in proportion to their length than the fossil. The Thorn Creek *S. schimperi* is more easily matched by leaves of *S. lasiandra.*

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 1174 (Lower Idaho), 2370 (Alturas); nos. 2371, 2372.

Salix wildcatensis Axelrod

Salix wildcatensis Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

The two willow leaves in the flora that are referred to this species are only slightly narrower than the specimen figured by Dorf, and closely resemble it in all other respects. They readily fall within the leaf variation displayed by the modern *Salix lasiolepis* Bentham, which is clearly related to the fossil species.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2373.

Family ULMACEAE

Ulmus moragensis new name

(Plate 48, figures 5, 7–9)

Ulmus brownellii Lesquereux. Dorf, Carnegie Inst. Wash. Pub. 412, I, p. 92, pl. 10, figs. 1–3, 10, 1930.

Small, asymmetrical elm leaves from three Middle Pliocene floras in California, the Alturas, Petaluma, and Lafayette Dam, seem sufficiently distinct from previously described fossil elms to warrant recognition of a new species. The following description is based on specimens from all three localities; the types are those figured by Dorf.

Description. Leaves strongly asymmetrically ovate and widest below, but the smaller specimens occasionally widest near the middle and only slightly asymmetrical; larger leaves 3.7 to 4.0 cm. long and (estimated) 3.0 cm. wide, smaller ones 1.5 to 2.0 cm. long and 1.1 to 1.3 cm. wide; petiole stout, up to 8 mm. preserved; midrib stout below and tapering above, sometimes slightly curved; larger leaves with 11 to 15 alternate pairs of closely spaced secondaries, smaller ones with 5 to 7, diverging at angles of from 80° to 85°, or in cases of strong asymmetry at 100°, in the lower part of the blade, to 15° or 20° above; entering marginal teeth or bifurcating to supply them; tertiaries coarse, often at right angles to the secondaries, and enclosing a finer coarse, polygonal mesh; teeth single-serrate in some instances, blunt, dentate, sometimes curved abaxially, the teeth sometimes obscurely toothed; texture coriaceous.

Discussion. Ulmus moragensis can be distinguished from *U. brownellii* Lesquereux by differences in marginal teeth, shape, and symmetry. In *U. brownellii* the single-serrate teeth are sharp and conical in shape, but those of *U. moragensis* are blunt and may show subsidiary teeth. The leaves of *brownellii* are commonly widest at the middle, whereas *moragensis* reaches maximum width in the lower part of the blade. In addition, the leaves of *U. moragensis* average smaller and are not so slender as those of *U. brownellii.*

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Chaney and Elias (1936, p. 39) have considered the California Pliocene specimens here placed in *U. moragensis* to be similar to *U. moorei* of the High Plains. The most important difference between these species is that *U. moorei* is typically symmetrical in shape; it also has distinctly single-serrate teeth of different shape from those of *U. moragensis*. The leaves of *U. moorei* are similar to those of the modern *U. crassifolia* Nuttall in adjacent Texas (see specimens in the U. S. National Herbarium).

It is difficult to evaluate the modern affinities of *U. moragensis* owing to the poor preservation of marginal characters. The types no longer reveal clearly whether the margin is completely single-serrate. Some of the Petaluma specimens, as well as the Alturas leaf, suggest that the marginal teeth may have subsidiary serrations. Among living species *U. moragensis* shows relationship to *U. pumila* Linnaeus of eastern Asia, which extends out into desert regions along watercourses. This species has a representative in the Pliocene of central Asia, *U. hedini* Chaney (1935*a*), but its leaves average larger than those of the California species. An essential similarity of Pliocene habitat cannot be doubted, however, when one takes into consideration the semiarid character of the climate in the two areas, and the dominance of riparian types in these floras.

Ulmus moragensis also resembles the smaller leaves of *U. americana* Linnaeus in the drier western parts of its range in the High Plains. As pointed out elsewhere in this chapter (p. 267), *U. moragensis* occurs in Middle Pliocene floras in west-central California, a region where the larger-leafed *U. californica* Lesquereux, which also resembles the leaves of *U. americana* in the drier western parts of its distribution, existed in Lower Pliocene time. The average leaf size of these species may be expressed as follows: *U. californica* 5.0 cm. long and 2.8 cm. wide (based on 26 specimens), *U. moragensis* 3.2 cm. long and 2.0 cm. wide (based on 10 specimens). Since *U. moragensis* is not known from Lower Pliocene and older floras at this latitude, it would appear that it may be a small-leafed derivative of *U. californica* which developed in response to increased aridity in post-Lower Pliocene time. But such an interpretation must await the collection of better-preserved material.

Judging from its description, *Ulmus monterreyensis* Muller, a recently discovered elm in the Sierra Madre Oriental of northeastern Mexico (Muller, 1942), also approximates the Middle Pliocene elm of California. This small-leafed species is reported to have characters resembling both *U. parvifolia* Jacquin of eastern Asia and *U. crassifolia* of Texas. Examination of specimens of *U. monterreyensis* may show it to be the modern equivalent of *U. moragensis*.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2374 (Alturas), 1696, 1697, 1698 (Petaluma).

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PLATES 47, 48

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FIG. 1. Cottonwood, aspen, and willow in yellow pine forest along Rush Creek, Modoc National Forest.

FIG. 2. Aspen, cottonwood, and willow on stream border, in open sagebrush country in eastern Oregon.

RIPARIAN VEGETATION RESEMBLING THE ALTURAS FLORA

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PLATE 48

Alturas, Lower Idaho, and Petaluma fossils

PAGE

Figs. 1, 2. *Salix vanorensis* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. ., nos. 1174, 2370 282

Fig. 3. *Populus payettensis* (Knowlton) Axelrod. Plesiotype. U. C. Mus. Pal., leobot. Ser., no. 2365 281

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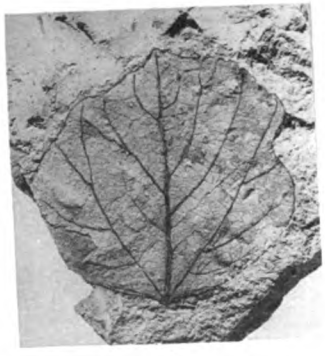

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PLATE 48

ALTURAS, LOWER IDAHO, AND PETALUMA FOSSILS

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The Dalles Flora

RALPH W. CHANEY

Introduction

The Dalles formation, lying upon the Columbia River basalt in the vicinity of The Dalles, Oregon, has yielded so fragmentary a fossil record that it has been variously assigned to horizons ranging from Upper Eocene to Pleistocene. When the writer first visited this region in 1916, no plant remains were found to add to the collection made by Thomas Condon in the sixties. Continued search during subsequent years led to the discovery of leaf impressions at the base of the Dalles formation on Chenoweth Creek. These were discussed briefly at a meeting of the Paleontological Society, where the Pliocene or Pleistocene age of the Dalles formation was suggested (Chaney, 1921*a*). A more extensive paper was submitted for publication at this time, but was later withdrawn when it was realized how little was known of the composition and sequence of other Cenozoic floras in western North America, and that the small collection could scarcely serve as a basis for reliable conclusions. During subsequent years Tertiary floras have been extensively studied in western North America. Starting with the floras of the John Day Basin, the writer and his associates have collected fossil plants from the major stratigraphic units of Oregon and adjacent states; numerous reports have been published, largely under the auspices of the Carnegie Institution of Washington. Other workers have added data of importance, especially in Washington and Idaho, until our knowledge of the stratigraphic and geographic range of Tertiary floras in the Pacific Northwest is relatively complete. It is now possible to refer the Dalles formation to the Pliocene, the age which was originally assigned to these beds by Condon.

The collection and study of fossil plants in eastern Oregon began with the arrival of Thomas Condon at The Dalles in 1862. An account of the early activities of this pioneer geologist, written by his daughter, Ellen Condon McCornack (1928), tells of his journeys into the John Day and Crooked River valleys, where he found plant and animal fossils at many localities now well known. Also recorded is his discovery of leaf impressions in the volcanic sediments of an old stone quarry near The Dalles. In 1869 Condon sent four small collections of plant fossils to Newberry, including nine specimens from the locality he designated as "Group C near The Dalles." These specimens, two of which still bear paper labels inscribed "Group C, Dalles, Oregon," represent all that was known of the flora of the Dalles group until the writer's visit to this area in 1920. In his letter to Newberry, dated February 28, 1869, Condon wrote as follows (McCornack, 1928, p. 46): " 'Group C' is from a sandstone at

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The Dalles. I have found in it four kinds of oaks and a very fine specimen of acacia, and within a few days a piece of fossil bone beautifully silicified was given me from the overlying rock."

It is worth adding here what is well known to students of earth history in western North America, that Condon showed a remarkable comprehension of the geologic record, not only at The Dalles, but widely throughout the state. Although Cope and others refer to his unpublished notes on the Dalles group, Condon's ideas were not brought together in print until the publication of his book *The Two Islands,* when he was over eighty years of age. Here he states (Condon, 1902, pp. 142–145):

Another of these Pliocene lake beds calls for notice and description. One standing on the streets of The Dalles and looking southward, will hardly fail to notice a well-defined ledge of gray sandstone set against the hills a mile or so from town, and extending westward three or four miles. It is a remnant of an old lake bed that once extended across the valley till its further margin set against the Klickitat mountains. What remains of this lake bed is today an unbroken level, although surrounded by many of the grandest exhibitions of volcanic and earthquake power, proving that no great violence has troubled the region since the waters of a quiet lake deposited its sediment there. All Miocene deposits are disturbed in Oregon. This deposit has not been disturbed; it must, therefore, have been deposited after the disturbance at the close of the Miocene, which would make it Pliocene. But more: a few years ago this rock was extensively used for building purposes in The Dalles. In one of the building blocks taken from the quarry was found a well-defined fragment of a metacarpal bone of a camel, and the camel in Oregon marks the Pliocene. This metacarpal of the camel became of added interest when a few years since a fragment of a very small radius was found, which came into the hands of the writer. This fossil was found among other bones, in an eastern extension of the same gray sandstone. The animal to which it belonged was an Auchenia of the camel family and represents an animal perhaps twenty-five to thirty inches in height.

Years ago the writer designated the group of rocks to which this gray sandstone belongs as The Dalles group and Pliocene.

There is a curious piece of geological history brought to the front in endeavoring to explain the circumstances under which this gray sandstone of The Dalles group must have been deposited in those far away Pliocene times. It today represents the bottom of a former lake. It is two hundred and fifty or three hundred feet above the present level of the Columbia River. The river has, in excavating its present bed, washed away the whole of that lake bed excepting this sandstone remnant, and worn its way through over two hundred feet of solid basalt besides, in reaching its present level. The east and south borders of this lake sediment are concealed by a covering of glacial deposit, under which it may be traced eastward two or three miles. It was from this eastward extension of the rock that the small Auchenia fragment of radius was found, and from this same gray sandstone Mr. D. H. Roberts obtained the distal end of a well-defined metacarpal bone of a larger Auchenia, perhaps the Vitakeri elsewhere noted.

From this same locality the writer, many years ago, made a collection of fossil plants which passed into the hands of Dr. Newbury. In this collection was a specimen of birch and a beautiful branch of Acacia, the leaflets all finely outlined upon the

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gray sandstone and the branch carrying three or four large thorns so distinctly impressed on the rock as to give a vivid impression of its place in plant life. Besides these, there was an intensely interesting group of oak leaves indicating a range of four or five different species, the whole collection leaving on the mind a conviction of a cold, unfriendly climate, producing a stunted growth of leaves.

Although Condon seems to have had only a casual familiarity with plants, he correctly interpreted the stratigraphic position and age of the Dalles formation, and even more remarkably the nature of the climate in eastern Oregon during the Pliocene epoch.

The fossil plants sent by Condon to Newberry in 1869 were given preliminary study, but were never discussed by Newberry in print. Apparently they were to have been included in his *Later extinct floras of North America* (1898), for a column is included in his table of distribution, pages 140–151, headed "Dalles of the Columbia, Oregon, Miocene (?)." No entries were made in this column, and Hollick, who edited the posthumous volume, apparently found no manuscript discussing the Dalles specimens. Newberry had prepared plates of them,[1] however, as mentioned by Knowlton (1902, p. 112) in the only published account of this material, here quoted:

> By the kindness of Dr. Arthur Hollick I have been enabled to examine a number of unpublished plates of fossil plants by the late Dr. Newberry, on which are depicted several species from the so-called Dalles group, at the Dalles of Columbia. The matrix, I am informed by Dr. Hollick, is a whitish, very coarse-grained volcanic ash, identical in appearance with that bearing fossil plants at Kelly Hollow, Wenas Valley, near Ellensburg, Washington. These plates were not published by Dr. Newberry and simply bear provisional names penciled on the margins of the plates. These species are represented as follows:
>
> *Acacia,* or *Cassia* sp.—A small, even-pinnate compound leaf of numerous small oblong leaflets. Nothing similar has been thus far found in the John Day Basin.
>
> *"Myrica diversifolia* Lesq."—Two figures of this form are shown. They appear to be the same as *Crataegus flavescens* Newb., from Bridge Creek.
>
> *"Ulmus* sp."—Two small, coarsely toothed leaves with well-marked secondaries ending in the marginal teeth. Judging from the drawings alone I should incline to refer these leaves to a small form of *Carpinus grandis* Unger, very similar to some forms found at Bridge Creek, and not to *Ulmus.* They are wholly unlike the common elm leaves that are abundant at this latter locality.
>
> With only these data available I should incline to regard the locality affording them as referable to the same age as the Bridge Creek beds, viz., Upper Clarno.

Knowlton's misinterpretation of the age of the Dalles flora was due to the fragmentary nature of the collection then available, and to his apparent lack of knowledge of the stratigraphic position of the Dalles formation. Additional reference will be made below to his redetermination of the specimens which Condon had sent to Newberry so many years before. In the light of studies now being conducted with George F. Beck, it is of particular interest that Hollick

[1] A recent inquiry at the library of the New York Botanical Garden indicates that the whereabouts of these plates is unknown.

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recognized a lithologic similarity between the Dalles and Ellensburg formations. This similarity is now known to extend also to the fossil floras from these two deposits.

Following the days of Condon, there is no record of additional fossil discoveries in the Dalles formation for nearly fifty years. During this interval the John Day Basin, with its relatively productive volcanic sediments, was the scene of extensive vertebrate collecting by Marsh, Cope,[2] Merriam, and Stock; and Bendire and Knowlton brought back large numbers of plant fossils to several eastern institutions. Renewed interest in the gorge of the Columbia River resulted from the studies of Williams and Bretz in 1916, and the problems presented in their papers (Williams, 1916; Bretz, 1917) have received increasing attention during the past two decades. But even during this relatively active stage of investigation, fossils have only rarely been collected in the Dalles formation. In 1927 Buwalda and Moore found a horse tooth, a proboscidean fragment, and a fused artiodactyl metapodial at a locality 2 miles southeast of The Dalles (1930, p. 16). More recently a well preserved left mandible of *Aelurodon* and fragmentary camel bones have been collected by Christ Fauerso on Chenoweth Creek near the fossil-plant locality, in association with silicified wood. It is apparent that conditions favoring the preservation of animals and plants were more limited in extent during the Dalles stage than during earlier Tertiary time in adjacent areas of Oregon and Washington.

Geologic Occurrence

The Dalles formation has been described by Piper (1932, p. 120) as "a heterogeneous series of semi-consolidated sandstone, sandy shale, conglomerate, fine-grained tuff, fine-grained tuffaceous sandstone, and coarse andesitic pyroclastic rocks." Largely pyroclastic in origin, these materials were reworked by streams and laid down as alluvial fans on the borders of the range of volcanoes which provided the eruptive products (Hodge, 1938, p. 864). The character of the sediments changes rapidly within a short vertical range as well as horizontally, with the finer sediments cross-bedded and in lenses. The coarser conglomerates and volcanic breccias are somewhat more constant in thickness over considerable areas, and are well indurated, forming the bluffs along the Columbia River near The Dalles and for 3 miles northwest to Chenoweth Creek. The maximum observed thickness of the Dalles formation in the lower valley of Chenoweth Creek is 762 feet, which represents approximately the lower half of the formation as a whole, and includes most of the coarser members. An erosional unconformity of slight relief separates it from weathered Columbia River basalt[3] in the bottom of a side valley which comes into the valley of Chenoweth Creek from the north in the NE. ¼ of Sec. 30, T. 2 N., R. 13 E.

Complete sections are given in a recent report on the geology of the Dalles

[2] The writer is unable to determine whether Cope visited this region himself, but collections were made under his direction by C. H. Sternberg and G. W. Sternberg in 1878, and by J. L. Wortman in 1879.

[3] Yakima basalt of Piper and other authors.

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region by Piper (1932, pp. 121–124), in which he includes a geologic map (pl. 11) and the most authoritative discussion of the Dalles formation as yet published. Piper indicates a maximum recorded thickness of 1500 feet along the divide between Mill and Threemile creeks, where the top of the formation is not represented. He states that the Dalles formation is separated from the basalt by "an erosional unconformity whose relief is about 100 feet in the Dalles region," and adds that "stratigraphic relations suggest that the lowest part of the formation may interfinger with the upper part of the Yakima basalt outside the area here described" (p. 125). This may have reference to one or more of the localities at which Warren (1941, p. 120) mentions interbedding of Hood River conglomerate, which he considers equivalent to the basal part of the Dalles formation, with the basalt. Warren further suggests (pp. 106–107, 119, 121) that the Columbia River (Yakima) basalt may be in part of Lower Pliocene age, the uppermost flows contemporaneous with the Dalles and Ellensburg formations. Beck (1940) has indicated his opinion that the Columbia lavas may have "accumulated without essential interruption throughout much of the late Tertiary." If it is true that the outpouring of basaltic lavas continued at least throughout the Miocene in the Columbia Gorge area and to the north, some of the upper flows must correspond in time to the Mascall formation, as exposed west of Dayville in the John Day Basin, 90 miles to the southeast. The flora and vertebrate fauna of the Mascall date it as definitely Miocene, and it has been variously assigned to the Middle and Upper stages of this epoch. Lower Pliocene rocks are not represented in the John Day Basin, where a gap between the Mascall and the Middle Pliocene Rattlesnake formation is represented by a structural unconformity (Merriam, 1902, p. 310; Merriam, Stock, and Moody, 1925, pp. 52–54). The suggestion that extrusion of basalt may have continued longer in areas north of the John Day Basin, perhaps extending into the Pliocene epoch, is consistent with the sections recorded. The estimated maximum thickness of the Columbia River lava is only 2500 feet in the John Day Basin (Collier, 1914, p. 10), as compared with 3700 feet in the Columbia Gorge (LeConte, 1874, p. 168), and as much as 4000 feet in eastern Washington (Russell, 1900, p. 134). Thus the basalt flows of the Columbia Gorge and eastern Washington may represent the time equivalent of the Columbia River basalt and the Mascall formation of the John Day Basin, and perhaps a part of the Lower Pliocene as well.

The structure of the Dalles formation is a subject of disagreement among recent workers. Bretz states (1917, p. 454) that it is "uptilted on the flank of the eastern anticline," the structure now termed the Ortley anticline. In their discussion of the Dalles and Hood River formations, Buwalda and Moore (1930, pp. 15, 17, 20) indicate that the Dalles formation and its equivalents are folded parallel with the Columbia River lavas. Piper (1932, p. 125) states that the Dalles strata "are nearly if not exactly parallel to the layers of the basalt, and the relief of the unconformity and the degree of weathering of the underlying basalt are little if any greater than in some of the erosional breaks within the basalt series." In the most recent paper referring to this problem, Warren (1941,

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p. 113) indicates his belief that the Hood River formation, which he considers essentially contemporaneous with at least the lower part of the Dalles and Ellensburg formations, is structurally conformable with the basalt. On the other hand, Condon's observations (1902, p. 143) support the opinion that the Dalles formation is horizontal and that it was deposited in a synclinal basin on the folded surface of the basalt. This viewpoint has recently been developed by Hodge (1938, pp. 860–869), who places the age of the Dalles formation anywhere from Middle Pliocene to Quaternary (pp. 834, 841, 865, 869), largely on the basis of its horizontal structure. There is certainly no paleontological support for an age reference later than Lower Pliocene, as will be indicated in our discussion of the age of the Dalles flora. If Hodge is to establish the soundness of his belief that the Dalles formation was laid down after the folding of the Columbia River basalt, and that its attitude is depositional rather than the result of folding, it will be necessary for him to explain (*a*) the position of the equivalent Hood River conglomerate below the top of the uppermost flow of basalt, (*b*) the range in elevation of the lower contact of the Hood River conglomerate from 200 to 4000 feet (Warren, 1941, p. 113; Bretz, 1917, p. 453), and (*c*) the scarcity in the Dalles formation of boulders of Columbia River basalt, which should certainly have been among the important constituents if it had been deposited on a folded basalt surface. The boulders and large cobbles of the Hood River conglomerate are invariably basalts, according to Warren (1941, p. 109), a fact which is consistent with his hypothesis that these deposits were laid down by the ancestral Columbia River in its course across the then unfolded Columbia River lava.

Another alternative may be suggested which seems better to explain the sequence of later Tertiary events than the assumption of either a post-orogeny or a pre-orogeny age for the Dalles formation, namely, that folding took place during the Dalles stage. In a world whose orderly sequence is of a different order from the orderliness of our textbooks and scientific papers, and often of our scientific thought, it is perhaps appropriate to suggest that events in earth history, the processes which bring them about, and their depositional or erosional consequences may not always coincide exactly with our arbitrary time divisions. The inception of conditions favoring the accumulation of andesitic pyroclastics may have preceded the opening phases of orogeny in this area. The beds of volcanic and fluvial conglomerate (basal Dalles and Hood River formations) would then have accumulated before, and perhaps in part during, the major folding which produced the present well defined structures in the Columbia River lava and overlying deposits to the west of The Dalles. The upper parts of the Dalles formation would have been laid down during or after the orogeny.

The more productive of the two plant localities (locality 3941) is situated near the foot of the south bank of Chenoweth Creek, just west of the point where the stream flows out onto the terrace of the Columbia River. (See plate 49.) This is in the west-central part of Sec. 29, T. 2 N., R. 13 E., about 2½ miles northwest of The Dalles. Here leaf impressions and a few imprints of fruits

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occur in a lens of light-colored, fine sandy tuff about 10 feet thick; this lens lies at about the middle of a 30-foot outcrop of cross-bedded sands and grits, and wedges out abruptly against the sandstone some 50 feet upstream. Leaves of similar types were collected 500 yards upstream, in another lens at a slightly higher stratigraphic level. Across the valley to the northwest, silicified wood from one or more stems has been obtained at a distance of 200 yards from the main leaf occurrence, in cross-bedded sands and grits like those associated with the leaves. All these plant collections are designated by the same locality number, 3941, and are in the Museum of Paleontology of the University of California. The *Aelurodon* and camel bones mentioned previously were found in a lens of fine tuff a few feet above the fossil wood and some 50 feet to the east. Field relations suggest that these deposits on the north side of the creek are at essentially the same horizon as that in which the leaves have been collected.

The material collected by Thomas Condon was obtained at a stone quarry whose exact location is not readily determinable. The writer has discussed the probable site of this quarry with several of the older residents of The Dalles, including Thomas Condon's nephew, Mr. J. W. Condon. The consensus of opinion is that it was situated on the cliff above the reservoir at the south-central edge of the city. On an excavated face here at an elevation of 650 feet, there is exposed a coarse, dark-colored sandstone resembling the matrix in which the Condon leaves are preserved. This sandy phase, some 90 feet in thickness, is well bedded, with thin seams of pumice lapillae. It overlies a coarse volcanic conglomerate, and is at a level approximately 400 feet above the base of the Dalles formation. The Pioneer Quarry, said to have been worked during the time Condon lived at The Dalles, lies a short distance to the east and at a slightly lower elevation; it seems a less likely source for the Condon collection than the cliff above mentioned, since the rock exposed in it is a blue-gray sandstone in no way resembling the matrix of the fossil specimens. Owing perhaps to the coarse texture of this matrix, the leaves are not so well preserved as those from the tuff on Chenoweth Creek. From the stone quarry above The Dalles came the "small fragment of radius" and the "distal end of a well defined metacarpal bone of a larger member of the camel family" which Condon mentions on page 94 of his noteworthy book, *Oregon geology* (1910). As was stated in the introduction to this chapter, the nine leaf-bearing slabs from this quarry were sent to Newberry in 1869, and are now a part of the collection of the New York Botanical Garden. Except for the brief comment by Knowlton quoted above (1902, p. 112) and their later mention by the writer in an abstract (1921), they are discussed for the first time in this report. I wish to express my appreciation to the officials of the New York Botanical Garden for submitting these specimens to me for study.

Although the material in the upper part of the Dalles formation averages of finer texture than that below, there are largely lacking the lenses of light-colored ash which provide the best matrix for plant preservation. The scarcity of this type of volcanic sediment may be due to reduced numbers of small lakes and

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other water-filled basins of accumulation in the valleys of later Dalles time. No fossils, either of plants or of animals, have been found in the upper part, and their comparative rarity even near the base is suggestive of a climate too dry for the rapid burial of organic remains below the upper limits of the water table. This is in striking contrast with the abundance of plant fossils in volcanic sediments of Miocene and earlier age in the John Day and Crooked River basins to the southeast. Conditions of deposition involving much-reduced rainfall are also indicated by the character of the Dalles flora, as will be mentioned in the section which follows.

The lithology, structure, and areal relations of the Dalles formation, and the composition of its flora, all suggest that it represents the time equivalent of the Ellensburg formation in eastern Washington, and of the Troutdale formation which is widely distributed in the lower valley of the Willamette River on the west side of the Cascades. All these formations are made up of volcanic sediments and pyroclastics which accumulated after the eruption of the Columbia River basalt had largely ceased, and which have been folded into the Cascade Range during subsequent orogeny.

Composition and Physical Indications

The Dalles flora as now known is made up of 12 species, all of which are dicotyledons.

Systematic List of Species

Spermatophyta
- Angiospermae
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Salix hesperia (Knowlton) Condit
        - Salix truckeana new species
    - Juglandales
      - Juglandaceae
        - Pterocarya oregoniana Chaney
    - Fagales
      - Fagaceae
        - Castanopsis sonomensis Axelrod
        - Quercus winstanleyi Chaney
    - Urticales
      - Ulmaceae
        - Ulmus californica Lesquereux
    - Rosales
      - Platanaceae
        - Platanus dissecta Lesquereux
      - Rosaceae
        - Prunus sp.
      - Leguminosae
        - Amorpha condoni new species
        - Cercis buchananensis Condit

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Sapindales
Aceraceae
Acer negundoides MacGinitie
Rhamnales
Vitaceae
Vitis sp.

A total of 193 specimens is available for study, including 32 on the nine slabs collected by Condon. With the exception of 12 samaras of box elder and the stem of *Prunus* sp., all these are leaves or leaflets; the latter are counted as separate units in table 26, which shows the numerical representation of the Dalles species.

TABLE 26

REPRESENTATION OF SPECIES AT THE DALLES LOCALITIES

Species	*Chenoweth Creek*	*Condon quarry*	*Total specimens*	*Per cent*
Acer negundoides:				
leaflets	108	5	125	64.73
fruits	12	0		
Amorpha condoni	0	23	23	11.92
Ulmus californica	10	0	10	5.19
Cercis buchananensis	4	3	7	3.64
Salix truckeana	7	0	7	3.64
Quercus winstanleyi	4	1	5	2.59
Salix hesperia	5	0	5	2.59
Platanus dissecta	4	0	4	2.07
Castanopsis sonomensis	3	0	3	1.55
Pterocarya oregoniana	2	0	2	1.04
Prunus sp.	1	0	1	0.52
Vitis sp.	1	0	1	0.52
Total	161	32	193	100.00

There is a predominant representation of box elders, even though we reduce the number of its leaf specimens to 38, on the assumption that the 113 leaflets may conceivably have been derived from this minimum number of complete leaves. On such a basis, we must also reduce the number of specimens of *Amorpha condoni* to 4, which is almost certainly the actual number of complete leaves represented, judging from their association on four slabs. With this reduction to a total of 99 complete plant units, box elder leaves and fruits still make up half of the specimens found. Only 3 species are represented by 10 or more leaves, and 5 forms are known from 4 or fewer specimens. It is apparent that without additional collections, it will not be possible to establish accurately the relative abundance of several members of the Dalles flora, or even to be sure that other species of plants may not have been present. The Ellensburg flora, from an area less than 100 miles north in Washington, is considered to represent essentially the same age as the Dalles. Most of the Dalles species have been

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found in it, and in addition, such species as *Celtis kansana* and *Populus alexanderi,* both of which might be expected in the Dalles flora. Unlike the latter, however, the Ellensburg flora has only a meager representation of *Acer negundoides.* Such local differences are in part due to accidents of collecting, but a more probable cause is an actual diversity of vegetation over short distances due to varied environments. The paucity of the fossil record in the Dalles formation is in marked contrast with the abundance of specimens in most Miocene and older floras of western North America, and is in itself a suggestion of the Pliocene age of the flora. In view of the fact that the material here described represents all the known collections over a period of nearly eighty years, it seems highly desirable to present without further delay the available evidence regarding the character and ecology of the Dalles assemblage, and the age of the beds in which it occurs.

In further contrast with many Miocene and older Tertiary floras of Oregon and adjacent states, a majority of the Dalles species find their modern equivalents in western North America, as shown in table 27. There is a rarity of genera now confined to eastern North America and Asia, with only *Ulmus* and *Pterocarya*

TABLE 27

ELEMENTS OF THE DALLES FLORA

Fossil species	*Equivalent living species*
West American Element	
Acer negundoides	A. negundo var. californicum Sargent
Amorpha condoni	A. californica Nuttall
Castanopsis sonomensis	C. chrysophylla A. DeCandolle
Cercis buchananensis	C. occidentalis Torrey
Platanus dissecta	P. racemosa Nuttall
Prunus sp.	P. spp.
Salix hesperia	S. lasiandra var. lancifolia Bebb
Salix truckeana	S. gooddingii Ball
Vitis sp.	V. californica Bentham
East American Element	
Acer negundoides	A. negundo Linnaeus
Amorpha condoni	A. fruticosa Linnaeus
Cercis buchananensis	C. canadensis Linnaeus
Platanus dissecta	P. occidentalis Linnaeus
Prunus sp.	P. spp.
Quercus winstanleyi	Q. prinus Linnaeus
Salix truckeana	S. nigra Marshall
Ulmus californica	U. americana Linnaeus
Vitis sp.	V. cordifolia Michaux
East Asian Element	
Acer negundoides	A. henryi Pax
Cercis buchananensis	C. chinensis Bunge
Prunus sp.	P. spp.
Pterocarya oregoniana	P. stenoptera DeCandolle
Quercus winstanleyi	Q. aliena Blume
Ulmus californica	U. pumila Linnaeus
Vitis sp.	V. spp.

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falling in this group.[4] Although the Dalles flora is typically western in character, most of its species also have living relatives on the eastern sides of the northern continents. It is readily apparent that this Pliocene forest, although retaining some members of the more generalized vegetation of earlier Tertiary epochs, was assuming an aspect much like that of the living forests of western North America.

Of the 9 species in the West American Element, there are 2 with modern equivalents, *Castanopsis chrysophylla* and *Salix lasiandra,* living in the immediate vicinity of the fossil localities. *Salix melanopsis* Nuttall, a modern species less like *S. truckeana* than *S. gooddingii* but obviously a closely similar form, is also found in the Dalles region. The chokecherry, *Prunus demissa,* may represent the equivalent of the wood designated as *Prunus* sp.

About 10 miles to the southeast in the valley of Eightmile Creek, *Acer negundo* (probably var. *interior* Sargent) has been noted under conditions which indicate that it is not native; this inference is consistent with the records of its known range, which limit it eastward, in the case of variety *interior,* to the mountains of Utah, and southward, variety *californicum,* to west-central California. The box elder grows successfully under cultivation, however, over all the range of its Tertiary equivalent, *A. negundoides,* which includes the Columbia Plateau and adjacent areas in western North America. Also growing in the valley of Eightmile Creek, about 7 miles from the Chenoweth Creek locality, is a colony of grapevines which has probably escaped from cultivation, though there is no evidence to that effect in its occurrence. *Vitis* has not been recorded as native in eastern Oregon. The California wild grape, *V. californica,* is known to range as far north as Grants Pass in southwestern Oregon. *Quercus garryana* Douglas, an abundant white oak now living at the fossil locality, can scarcely be considered to represent a modern descendant of *Q. winstanleyi.* The leaves of this fossil species are simply lobed, with shallower sinuses than those of *Q. garryana,* more closely resembling those of *Q. prinus* of the eastern United States, and of *Q. aliena* of northeastern Asia. With these relations in mind, the oak from the Dalles flora has been placed in the East American and East Asian Elements. Another western white oak, *Q. lobata* Née, is now limited to western California, as far north as the upper valley of the Sacramento River. As noted in the introductory chapter, its juvenile leaves may closely resemble those of *Q. winstanleyi* in being shallow-lobed and simple-lobed, but the number of lobes on such leaves is smaller than on the fossil leaves.

The 3 remaining species of the West American Element, *Amorpha condoni, Cercis buchananensis,* and *Platanus dissecta,* no longer have generic representatives in Oregon. Two of the related living species, *Cercis occidentalis* and *Platanus racemosa,* have their northern limits in the upper valley of the Sacramento River, and *Amorpha californica* ranges only as far north as central California. The centers of distribution of these 3 species in California all lie well to the south. In reconstructing the environment occupied by the Dalles flora,

[4] These genera occur elsewhere in the northern hemisphere, but the above-mentioned regions are the only parts of their ranges relevant to the present discussion.

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we shall take into consideration the factors which have resulted in the elimination from eastern Oregon of more than half the plants known to have lived there during early Pliocene time. The first approach to the solution of this problem will involve a consideration of the physical setting in the valley of Putah Creek, in central California, where all the modern equivalents of the Dalles West American Element are now living in close proximity.

Putah Creek flows southward in eastern Napa County, turning east a few miles south of Monticello, crossing the Inner Coast Range, and continuing east through Winters across the flood plain of the Sacramento River. Its valley is narrow and steep-sided where it crosses the Inner Coast Range, broadening out to the east with relatively low bordering slopes. To the west of its course in Napa County, the Napa Range rises to an elevation of from 1700 feet to over 4000 feet along its crest, and constitutes the principal topographic barrier between the coastward slopes of the Coast Ranges and the Great Valley. In chapter 13, pages 358–360, the vegetation of these coastward slopes will be contrasted with that along the course of Putah Creek between Monticello and Winters. On the stream borders in this region, box elder (*Acer negundo* var. *californicum* Sargent) is locally predominant, and redbud (*Cercis occidentalis* Torrey) widely distributed on the flood plain and adjacent slopes. There are also big-leaf maple (*Acer macrophyllum* Pursh), buttonbush (*Cephalanthus occidentalis* Linnaeus), Oregon ash (*Fraxinus oregona* Nuttall), California black walnut (*Juglans hindsii* Jepson), toyon (*Photinia arbutifolia* Lindley), Fremont cottonwood (*Populus fremontii* Watson), black willow (*Salix gooddingii* Ball), yellow willow (*Salix lasiandra* Bentham), and California wild grape (*Vitis californica* Bentham). Western sycamore (*Platanus racemosa* Nuttall) is reported by Jepson to occur farther downstream (oral communication, February 27, 1941). On slopes adjacent to the valley, oaks (*Quercus agrifolia* Née, *Q. douglasii* Hooker and Arnott, *Q. dumosa* Nuttall, *Q. wislizenii* A. DeCandolle, and *Q. lobata* Née, with the last named also extending down onto the flood plain), digger pine (*Pinus sabiniana* Douglas), and hollyleaf cherry (*Prunus ilicifolia* Walpers) are numerous, and mock locust (*Amorpha californica* Nuttall) is present in ravines. Chinquapin (*Castanopsis chrysophylla* A. DeCandolle) occurs on higher slopes of the adjacent Vaca Mountains to the south. Of the woody plants above mentioned, the following are represented by equivalent species in the Dalles flora:

Dalles species	*Modern species of Putah Creek*
Acer negundoides	A. negundo var. californicum
Amorpha condoni	A. californica
Castanopsis sonomensis	C. chrysophylla
Cercis buchananensis	C. occidentalis
Platanus dissecta	P. racemosa
Prunus sp.	P. ilicifolia
Salix hesperia	S. lasiandra
Salix truckeana	S. gooddingii
Vitis sp.	V. californica

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The absence of such shrubs as buttonbush and toyon from the Dalles flora is not surprising, for even where they occur their leaves seem rarely to enter the sedimentary record, either of today or of the Tertiary. Neither walnut nor cottonwood is common along Putah Creek, and Oregon ash is not abundant. The only abundant species of the living flora which has no representative in the Dalles is the valley oak, *Quercus lobata.* As stated above, this species may have leaves similar to those of the fossil *Q. winstanleyi,* but they commonly show sufficient differences to indicate that there is little if any relationship. From the paucity of its record in the Dalles formation, *Q. winstanleyi* may be supposed to have occupied a position on slopes above the valley, as does *Q. lobata,* and to have represented an approximate ecologic equivalent of this modern species. We may conclude that the Dalles flora includes representatives of the more characteristic and readily preservable species of the vegetation living along the stream in this modern valley, as well as of several species occupying adjacent slopes. A survey of the climate in the Putah region today should therefore throw some light on the Pliocene environment of the Dalles flora.

No climatic data are available for the immediate vicinity of the Putah Creek locality, but approximate estimates of temperature and precipitation are based on the figures for stations at Brooks and Vacaville, lying to the north and south, and both situated east of the Coast Ranges. These estimates, together with data for The Dalles and for two stations in Nebraska, are presented in table 28.

TABLE 28

CLIMATIC DATA FOR STATIONS USED IN COMPARISONS WITH THE DALLES FLORA

MONTH	MONTHLY AND ANNUAL AV. TEMPERATURE (°F.)				MONTHLY AND ANNUAL AV. PRECIPITATION (IN.)			
	Dalles	Putah Creek Valley*	Beatrice	Chadron	Dalles	Putah Creek Valley†	Beatrice	Chadron
January....	32.4	46.0	24.4	22.0	3.01	4.10	0.60	0.68
February...	38.1	50.7	27.2	28.3	2.03	4.40	1.00	0.65
March.....	46.0	53.7	39.2	35.8	1.37	2.81	1.40	0.99
April.....	53.4	57.0	51.8	46.0	0.67	1.92	2.62	2.57
May.....	60.3	63.8	61.7	55.8	0.62	0.65	3.97	2.86
June.....	66.5	68.7	71.3	66.2	0.51	0.14	4.17	2.92
July.....	72.5	74.9	77.2	73.8	0.20	0.00	4.03	2.87
August.....	71.5	73.8	75.1	71.8	0.19	0.02	3.51	1.67
September..	63.0	69.8	66.8	62.2	0.79	0.25	2.87	1.40
October....	53.3	63.1	54.0	49.4	1.04	1.09	2.08	1.47
November..	42.5	54.3	39.6	36.6	2.53	2.74	1.23	0.91
December..	35.3	47.2	27.4	25.7	2.96	4.33	0.89	0.61
Annual...	52.9	60.3	51.3	47.9	15.92‡	22.36‡	28.37‡	19.60‡

*Figures from Vacaville, California.

†Figures represent averages of Brooks and Vacaville.

‡Total.

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It need scarcely be noted that the climatic data of this table may be highly misleading if considered without due analysis. The average temperature at The Dalles, although essentially the same as at Beatrice, has a much lower seasonal range, intermediate between Beatrice and Putah Creek. At Beatrice most of the winter precipitation occurs as snow, in contrast with conditions at The Dalles, where rain falls during the mild winters.

Like The Dalles, where 81 per cent of the total falls from October through March, the Putah Creek region is characterized by winter rainfall, with the annual total some 6 inches more than at the Oregon station. The temperature is much higher than at The Dalles, as might be expected from the lower latitude of central California; its greater uniformity from season to season appears to result in large part from closer proximity to the ocean. On the basis of these comparisons, there appears to have been a marked reduction in rainfall and temperature in the Dalles area since the Pliocene. Such changes in climate, especially in the temperature factor, appear responsible for the elimination of *Amorpha, Cercis, Platanus,* and *Vitis* from the modern vegetation of eastern Oregon, since these genera have their best development in warmer regions. The absence of box elder from the Dalles region today is difficult to explain, since this species survives elsewhere under climatic conditions similar to those now found there; shrinkage discontinuity due to progressive aridity seems the most plausible explanation. Reasons for the post-Pliocene disappearance of *Ulmus* and other members of the Dalles flora no longer living in western North America will be considered below in our discussion of the East American and East Asian Elements. The presence of these elements in the Dalles flora suggests that the environment which it occupied differed in certain essential respects from that of the Putah Creek region today.

As was indicated in table 27, several species referred to the West American Element may equally well be assigned to the East American Element. The *Platanus* material is too fragmentary to indicate whether its relationship is closer to the living *P. occidentalis* of the eastern United States, or to *P. racemosa* of the West; abundant specimens from the closely related Ellensburg flora, however, indicate a greater resemblance to the eastern species. In their large size and the openly cordate shape of their bases, the leaves of our fossil redbud resemble those of *Cercis canadensis* of the eastern United States, although their rounded tips also suggest relationship to the western *C. occidentalis.* Our leaflet impressions of box elder show coarse marginal characters which suggest their equivalence with the western variety *californicum* rather than with the eastern *Acer negundo.* Fossil material of *Amorpha* and *Vitis* is not sufficiently well preserved to afford a basis for choosing between eastern and western species for modern equivalents. Judging from other known characteristics and relationships of Tertiary plants, it is fair to assume that there may have been less difference between eastern and western representatives of these genera during the Pliocene than today. Interrelations of our Oregon specimens with living species on both sides of the continent are in that case to be expected, and make desirable

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some further analysis and comparison of the environment occupied by living equivalents of Dalles species in the region east of the Cordillera.

Several of the modern equivalents of the East American Element have the western limits of their ranges in Nebraska. *Acer negundo*,[5] *Cercis canadensis*, and *Platanus occidentalis* extend westward into southeastern Nebraska. *Amorpha fruticosa*, *Salix nigra*, *Ulmus americana*, and *Vitis* spp. also occur here, ranging west across the state. *Quercus prinus* has its nearest approach in the valley of the Mississippi River in southeastern Missouri, but other white oaks, such as *Q. muhlenbergii* and *Q. bicolor*, show many leaves similar to our fossil *Q. winstanleyi*, and have their westward limits in southeastern Nebraska. *Quercus macrocarpa*, less like *Q. winstanleyi* but with occasional leaves of the same sort, ranges across the state to the northwest and into Wyoming. It seems apparent that the vegetation of this region, some 1300 miles east-southeast of The Dalles, has much in common both with the present-day riparian vegetation in the valley of Putah Creek and with the Pliocene vegetation of eastern Oregon.

The modern forests of Nebraska deserve further consideration at this point because they throw light on the development of vegetation in North America. The discussion of their relation to other vegetation, living and fossil, presents a significant illustration of the sort of problem which faces the paleobotanist when he attempts to establish floral relationships across wide intervals both in space and in time. When Nebraska forests as a whole are compared with the Dalles flora, differences more striking than the similarities above mentioned are at once apparent. Making up a conspicuous part of the vegetation in the southeastern part of the state are numerous broad-leafed deciduous genera not represented in the Dalles flora; these include *Carpinus*, *Diospyros*, *Hicoria*, *Morus*, *Ostrya*, *Sassafras*, and *Tilia*. *Fagus* is present in adjacent Iowa and Missouri, and *Castanea*, *Catalpa*, *Liquidambar*, *Liriodendron*, *Magnolia*, and *Nyssa* occur in Missouri and Illinois within an average distance of 200 miles. Anyone familiar with the Tertiary vegetation of the Columbia Plateau will recognize at once the resemblance of this assemblage to the Bridge Creek, Mascall, and Latah floras. Lacking from this Nebraska forest is the distinctive *Sequoia*, but *Taxodium*, a common member of the Mascall and Latah, is found in Missouri and Illinois within 200 miles.

Such a resemblance is consistent with our belief that the modern vegetation of the eastern United States and the Miocene floras of the western United States had a common northern origin. During the Miocene and earlier epochs of the Tertiary, absence of such mountain barriers as the Cascades and Coast Ranges resulted in the extension of mild, moist climates inland across the Columbia Plateau. With ample summer rainfall during the Miocene (LaMotte, 1936, p. 94), broad-leafed deciduous angiosperms together with *Sequoia* and *Taxodium* were widely distributed over this region. Evidence has been presented that this flora moved down into the western United States from the north, and from the uplands of middle latitudes, as a result of progressive reduction in tempera-

[5] A variety *interior* is widely distributed in the Rocky Mountains.

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ture and rainfall inaugurated at the close of the Eocene or shortly thereafter (Chaney, 1936*b*, pp. 72–73). Similar conclusions were reached many years ago regarding the Tertiary floras of Europe (Gardner, 1879, p. 125), and have recently been presented for the Tertiary floras of Asia (Chaney and Hu, 1940, pp. 117–138). The broad-leafed deciduous forests of the eastern United States unquestionably had a similar northern origin. But unlike the Miocene floras of Oregon and Washington, they have survived down to the present in the area east of the Rockies because of the persistence there of a climate with rainfall well distributed throughout the year, especially during the summer months. Resemblance of the living vegetation of southeastern Nebraska to the Miocene floras of western North America is therefore both an expression of their common origin and a measure of the climatic changes which have altered the environment on the west side of the continent since the Miocene.

The less marked relationship of the Nebraska forest to the post-Miocene Dalles flora follows naturally from the restricting effects of climatic change in western North America during Pliocene time. With the building of a range of volcanic peaks, summer rainfall was reduced in the area to the east, and only the more hardy trees of the Miocene forests, such as box elder, elm, redbud, sycamore, and willow, survived into the Pliocene; *Ulmus* has subsequently become extinct from the Rocky Mountains westward, and none of the others above named except *Salix* have survived in the Dalles region. The presence of these same hardy genera in the living forest of southeastern Nebraska is of interest for comparison with the Dalles flora. But since they occur there in a minority, with genera which require more ample moisture, no close resemblance is indicated between the vegetation as a whole and the Dalles flora. If at some future time there is a marked reduction of rainfall in southeastern Nebraska, such typically "Miocene" genera as *Carpinus, Hicoria, Ostrya,* and *Tilia* will doubtless be eliminated, leaving the vegetation essentially like that which lived in eastern Oregon during early Pliocene time. In the meantime the forest of southeastern Nebraska must be considered to represent a relatively humid type of vegetation, and one requiring more uniformly distributed precipitation than does the Dalles flora. There is little basis for believing that Pliocene climate in eastern Oregon was closely similar to that of southeastern Nebraska today.

Comparison may also be made between the Dalles flora and the riparian vegetation of western Nebraska, where the rainfall is much less and winter temperatures are lower than in the southeastern part of the state. Several of the hardiest Dalles equivalents, such as elm, willow, and oak (the somewhat less closely related *Quercus macrocarpa*), have their extreme western limits in this region. Lower winter temperature and a different precipitation regime seem adequate to account for differences between the modern vegetation of western Nebraska and the Dalles flora, differences more conspicuous than their similarities.

While the historical significance of the vegetation of Nebraska and adjacent areas is under consideration, it may be profitable to review the relationships between this modern forest and the other Tertiary floras of western North America. Such floras as the Mascall and Latah contain the following types of

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plants not represented in southeastern Nebraska today: (1) conifers, including *Abies, Libocedrus, Picea, Pseudotsuga, Sequoia, Taxodium, Taxus, Torreya,* and *Tsuga,* now largely confined in North America to more northerly or mountainous regions, or to the Pacific coast;[6] (2) warm-temperate to subtropical angiosperms (our Caribbean Element), including such American genera as *Cedrela, Gordonia, Oreopanax,* and *Tetracera,* some of which genera occur also in Asia; and (3) a group of temperate to subtropical genera now restricted to Asia (our East Asian Element), including *Ailanthus, Cercidiphyllum, Dipteronia, Engelhardtia, Ginkgo, Keteleeria, Trapa,* and *Zelkova.*

The absence of these Asiatic genera from the modern vegetation of Nebraska may perhaps be explained by the failure of most of them to reach the region east of the Rocky Mountains during the Tertiary period. *Trapa,* however, is recorded in the Pliocene Citronelle formation of Alabama (Berry, 1916*b*, p. 203), and leaves considered referable to *Cercidiphyllum* are of common occurrence in the Wilcox Eocene of the Gulf states (Brown, 1939, p. 493). Possibly most of what we consider the East Asian Element, on the basis of the survival of modern equivalents in Asia, may once have ranged widely across North America as did *Trapa* and *Cercidiphyllum*. The reasons for the extinction of these genera on our continent and for their survival in Asia are unknown, though if such genera are gradually becoming extinct in our day they might be expected to linger on longer in some areas than in others. The record of the Miocene, when members of the East Asian Element may have been numerous in the eastern United States, is unfortunately meager. Few volcanoes were showering the area east of the Rockies with ash at this time, and subsequent glaciation has removed or buried any Tertiary deposits which may have accumulated as far east as southeastern Nebraska. The resulting lack of direct evidence regarding the character and distribution of Tertiary forests in the upper Mississippi Basin renders all the more valuable such inferences as may be drawn from the resemblances of the modern forests there to Miocene and Pliocene floras in western North America.

It is not possible to determine whether conifers were formerly more abundant in this area than they are today. Even in the Miocene forest of the Columbia Plateau they seem not to have been numerous, with the exception of *Sequoia* and *Taxodium*. Whether the present restriction of conifers to more northerly or mountainous habitats in the eastern United States has taken place in comparatively late geologic time, or whether the climate and topography of Nebraska have been relatively unfavorable to them as far back as the Miocene, there is no present means of determining. It seems probable that the vegetation of that epoch may have included more conifers, and perhaps more Asiatic genera, than it does today. The present distribution of *Taxodium distichum* Richards up the valleys of the Mississippi and Ohio rivers, and up the Wabash River almost to the latitude of southern Nebraska, is suggestive of its former wider occurrence under milder temperature conditions. But there is no basis for sup-

[6] *Pinus ponderosa* Douglas has its eastern limits in central Nebraska, and *Juniperus virginiana* Linnaeus is widespread over the eastern part of the state.

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posing that conifers and genera now limited to Asia were as numerous east of the Cordillera as in Oregon and Washington during the Miocene.

Referring to the warm-temperate and tropical American genera listed above, it seems reasonable to assume that they, like *Taxodium,* may have continued to live along the Atlantic and Gulf coasts throughout later Tertiary time as relicts from the Eocene, extending inland up the stream courses as did genera of similar types in western North America during the Miocene (Chaney, 1938*c,* pp. 641–647). Boundaries of the older Tertiary plant-bearing formations in the lower Mississippi Valley have been mapped by Stephenson (see Berry, 1915, figs. 28–31; 1924, fig. 1) and by Matson (1916, fig. 15). These indicate fluctuations in position of the shore line from latitude 35° to 37° north. Berry has made the following significant statement regarding Tertiary climates in this region (1924, p. 25):

> As I interpret the evidence, there appears to have been a steady progression throughout the Eocene in this area toward more tropical conditions. The Upper Cretaceous floras suggest the existing warm temperate rain forest, those of the lower Eocene are similar but indicative of slightly warmer climate, and those of the middle Eocene are intermediate between subtropical and tropical. The upper Eocene and lower Oligocene floras in this region are still more tropical in character, after which time the climatic curve seems to have descended until the conditions gradually approximated those that prevail at the present time in these latitudes.

The Eocene and Oligocene floras which are the basis for Berry's conclusions are of a much more tropical type than the Latah and Mascall, or than any other Miocene floras known from the United States. Their occurrence in western Kentucky, southwestern Missouri, and eastern Arkansas suggests that Eocene forests to the north in Nebraska may have contained many warm-temperate and subtropical genera which have subsequently disappeared. Some of the more hardy of these doubtless lingered on into the Miocene, and modern representatives such as *Asimina triloba* Dunal, *Morus rubra* Linnaeus, *Lindera aestivale* (Linnaeus) Nees, *Sassafras variifolium* (Salisbury) Kuntze, *Celastrus scandens* Linnaeus, *Menispermum canadense* Linnaeus, *Aristolochia macrophylla* Lambert, *Euonymus atropurpureus* Jacquin, and *Smilax* spp. still live in Nebraska or in immediately adjacent areas. It is worthy of note that these are all shrubs or vines, for this habit in the under-story layers of a forest is especially favorable for survival. The modern occurrence of *Bumelia lanuginosa* (Michaux) Persoon, *Hicoria pecan* (Marshall) Britton, *Ilex opaca* Aiton, *Nyssa aquatica* Linnaeus, *Planera aquatica* (Walter) Gmelin, *Quercus phellos* Linnaeus, and *Q. prinus* Linnaeus, and of *Taxodium distichum* as already mentioned, along the valleys of the Mississippi River and its tributaries from the Gulf of Mexico to Missouri and Illinois is an example of the northward extension of other typically southern species today.

Along the Atlantic and Gulf coasts, *Ilex* now ranges from Massachusetts to Texas; *Taxodium* from New Jersey to Texas; *Persea* from Delaware to Texas; *Cyrilla, Nyssa,* and *Xanthoxylum* from Virginia to Texas; *Styrax* from Virginia

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to Louisiana; *Cliftonia* from South Carolina to Louisiana; and *Gordonia* from Virginia to Mississippi.

It would be misleading to imply that these Eocene relicts, most of which are members of families largely tropical in distribution, extended as far north as they do today throughout the Cenozoic era. For the fluctuating temperatures of the Pleistocene are known to have shifted the ranges of many trees southward during glacial stages, and northward during interglacial. Such northern conifers as *Larix laricina* Koch and *Picea glauca* Voss are recorded from deposits of probable early Wisconsin age from southern Louisiana, nearly a thousand miles south of their present southern limits (C. A. Brown, 1938, pp. 66–68). Records of *Asimina triloba* and *Maclura aurantiaca* Nuttall in the Don Valley interglacial beds of Toronto (Penhallow, 1900) and of *Taxodium distichum* as far north as New Jersey (Berry, 1923, p. 66) indicate somewhat more favorable climatic conditions than those now characterizing these regions. Since eastern Nebraska was covered by a continental glacier during part of the Pleistocene, its vegetation must have been profoundly affected at that time, and the composition of its modern forest must have been conditioned by extensive migrations across this Pleistocene ecotonal zone. It seems justifiable to assume, however, that many of the trees now found in the upper Mississippi Valley were represented there by equivalent species during at least later Tertiary time, and that their present distribution and association represent a return to their approximate Miocene positions since the last stage of glaciation. The general aspect of the vegetation of southeastern Nebraska, and its marked relationship to the Miocene floras of western North America, are consistent with such an assumption.

This discussion, which has led to our consideration of forests far removed in location and composition from the Dalles flora, indicates the fallacy of attempting to establish the age of a fossil flora through the occurrence in it of a small number of similar or identical species. This is especially the case if the floras compared come from regions as widely separated as Oregon and Nebraska. If instead of the living vegetation of the latter region we had for comparison only detached leaves, fruits, and stem fragments, it would be possible to match a sufficient number of the Dalles and Nebraska specimens to suggest a correlation of the sort often accepted as adequate. But if our comparison involved not only the species or genera which appear in both, but recognition of the absence from the Dalles flora of many humid types of broad-leafed deciduous trees of the Nebraska assemblage, a wide difference would at once be established. If the Dalles material comprised only the meager fragments so often brought in by the geologist, there might be some question whether the absence of the humid genera was not a reflection of incomplete collecting; but a sufficient number of specimens are now at hand to indicate that such genera were not members of the Dalles assemblage. The two floras could therefore be readily distinguished, and the conclusion would be reached that they occur in deposits either of different age, or from widely separated localities.

One further difficulty might arise if our knowledge of the existing vegetation

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of southeastern Nebraska were based only on impressions of leaves and fruits. The predominance in this flora of broad-leafed deciduous genera might lead a student of western Tertiary floras to conclude that it was of Miocene age. Only through an understanding of the rarity in or absence from the Nebraska flora of certain types of plants characteristic of Miocene floras—*Sequoia* and most other conifers, the group of temperate genera now confined to Asia, and the warm-temperate to subtropical genera—would it be possible to reach a sound conclusion regarding its age relations to the Mascall and Latah floras of the Columbia Plateau. This comparative method, now generally employed in American studies, may be expected to eliminate many of the stratigraphic inconsistencies which have brought confusion in the past, and to provide a better understanding of the changes in vegetation through time and across wide areas.

There remains for brief consideration the East Asian Element of the Dalles flora, comprising 7 species, as shown in table 27, whose living equivalents range from southeast and central China to north China, Manchuria, Korea, and Japan. One of these, *Pterocarya oregoniana,* is not generically represented in North America today. The remainder have been listed in the other elements, since they also have living equivalents in western and eastern United States. In the case of *Cercis buchananensis* and *Quercus winstanleyi,* resemblance to living Asiatic species is fully as close as to American ones. *Prunus* and *Vitis* are represented by such incomplete material in the Dalles flora that only the most general of relationships may be indicated. *Ulmus californica* seems much more similar to the American *U. americana* than to the Asiatic *U. pumila,* and *Acer negundoides* is likewise more similar to *A. negundo* var. *californicum* than to *A. henryi.* The climate of the regions occupied by these living species of eastern Asia is essentially like that of the eastern United States, with summer rainfall and seasonal extremes of temperature. In fact, for the purposes of our analysis, the East Asian and East American Elements may well be considered together; modern equivalents of the species in both elements occupy regions with higher, more uniformly distributed rainfall than characterizes the valley of Putah Creek and other localities where living equivalents of the Dalles flora are found in the western United States. For the most part these modern equivalents in Asia are marginal members of forests with more mesic requirements, hardier types which might be expected to survive in that region if future climatic changes were to bring lessened precipitation and greater extremes of rainfall and temperature. As in the case of the East American Element, the presence of this East Asian Element in the Dalles flora does not indicate a forest or a climate closely similar to those now found in eastern Asia, for the modern equivalent species represent only a small part of the Asian forest as a whole. The problem regarding the physical setting of the Dalles flora must be solved by consideration of all three environments in which modern relationships are apparent: eastern Asia, the eastern border of the Great Plains in North America, and Putah Creek on the inner margin of the Coast Ranges of California.

When we compare the Dalles flora with the living vegetation of these three

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regions, it becomes readily apparent that it shows a closer resemblance to that now living in the valley of Putah Creek than to the forests on the eastern sides of the continents. Most of the characteristic species of the Coast Range locality have fossil equivalents in the Dalles flora, whereas only small parts of the forests of Nebraska and China are represented. The estimated precipitation at the Putah Creek locality is 22 inches a year, of which 90 per cent falls in the months from October through April; summer temperatures are not greatly different from those shown for other stations (see table 28), but winter temperatures are somewhat lower at The Dalles, and much lower at the Nebraska localities. We conclude that the climate in the area occupied by the Dalles flora during the Lower Pliocene was of the same general order as that found in the Inner Coast Ranges of central California today.

The sparse occurrence in the Dalles flora of three species, *Pterocarya oregoniana, Quercus winstanleyi,* and *Ulmus californica,* whose living equivalents no longer live in western North America but are found on the eastern sides of the continents is considered an adequate basis for modifying somewhat our ideas on the Pliocene climate in this part of eastern Oregon. These species live under conditions more similar to those described for eastern Nebraska. In addition, such species as *Cercis buchananensis* and *Platanus dissecta* seem more closely related to modern species of eastern than of western North America, and there are other cases in which the relationship is equally close. With this small group of at least 3 species suggesting climate with higher summer rainfall, and perhaps with lower winter temperatures, than are now found in the valley of Putah Creek, our concept of the Pliocene climate in eastern Oregon, as based only on comparisons with this region, must be somewhat altered. Summer showers were probably of regular occurrence, and the total annual rainfall may have been as high as 25 inches. Winter temperatures may have reached somewhat lower levels than in the Putah Creek valley today, although the generally southern occurrence of modern equivalents both in western North America and in eastern Asia is not consistent with an assumption that they were regularly subjected to freezing temperatures. The bearing of topographic relations on this problem of local climate will be considered below.

Evidence is presented in chapter 12, page 331, that the rainfall regime of the Miocene, involving regular summer showers, extended on into the Pliocene in other parts of western North America, and that it was progressively reduced from the interior toward the coast. The role of orogeny in this climatic trend will be emphasized in our concluding chapter. At this point it may appropriately be mentioned that the diastrophic and volcanic events which resulted in the upbuilding of the Cascade Range during Pliocene and subsequent time appear to have been a principal factor in the climatic changes which eliminated from the Dalles region, and from all of western North America, many of the angiosperms characteristic of the Miocene floras there. The survival of a few of these into the Pliocene of eastern Oregon is consistent with geologic evidence that the climatic barrier interposed by the Cascade Range had not reached its present effective height during the Dalles stage, in the early part of the epoch.

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The Dalles flora represents a typically riparian assemblage as judged by its relationship to the modern vegetation of Putah Creek. Box elder was the dominant tree, at least in the immediate area of our principal fossil locality, with elm, grape, redbud, sycamore, and willows also growing along the stream borders. White oak and chinquapin were probably distributed on adjacent slopes, judging by the occurrence of their modern equivalents in Oregon and by their rarity in the record. *Cercis* may also have been a slope species, together with *Amorpha* and *Pterocarya*. Not only the habitats of related living plants, but the characteristics of the sediments in which they occur indicate a valley environment. Evidence of sorting may commonly be noted throughout most of the Dalles section, coarse layers alternating with finer materials, lenses of ash and gravel pinching out abruptly. Close proximity to volcanic sources is suggested by the coarse angularity of the volcanic agglomerates, some of which appear to have been deposited as mudflows. The plant fossils from the quarry where Condon collected are in a gritty sandstone which is interpreted to represent torrential flood-plain deposits. At the Chenoweth Creek locality, fossil plants occur in a relatively fine member near the base of the formation. Here the sands are cross-bedded, and there are several lenses of ashy tuff. One of these lenses, from which most of our leaf impressions were collected, is 10 feet thick, and wedges out so abruptly against the sandstone at the west as to suggest that the ash was deposited in a lake basin on the sandy floor of a valley, or perhaps along the channel of a fan. Elsewhere in the Dalles formation there are abrupt changes in the texture of the sediments which imply fluctuating conditions of deposition with at least temporary high velocity of the streams involved.

This lithology suggests precipitation not unlike that in eastern Oregon today, where torrential summer rains build up fans of coarse debris at the mouths of tributaries to such rivers as the John Day and Deschutes. These coarse deposits extend out upon the finer sediments of the flood plains of the major streams, differing in aspect from those of the Dalles formation only in being generally better assorted and in containing less angular boulders and cobbles. Doubtless the rainfall during the Dalles stage fluctuated even more widely than it does today as a result of the heavy showers incidental to the eruption of adjacent volcanoes. There is also evidence from the plant fossils that there was a larger amount of summer and of annual precipitation than now falls in this region.

Occurrence of such species as *Pterocarya oregoniana, Quercus winstanleyi,* and *Ulmus californica* in small numbers also has a significant bearing on our reconstruction of the topographic setting. As will be set forth in the chapter which follows, all three of these species are more abundant in the Troutdale flora from beds of essentially the same age in western Oregon. Valleys like that of the existing Columbia River still permit the extension of such modern coastal species as *Acer circinatum, Castanopsis chrysophylla,* and *Quercus garryana* inland through the Cascade Range into eastern Oregon. The presence of the above-mentioned species in the Dalles flora, together with *Castanopsis*

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sonomensis, is strongly indicative of a valley across the growing volcanic range, along whose course an eastward extension of coastal conditions made possible the existence of trees more typical of the western slopes. The sparse representation of these species in the Dalles flora is consistent with our suggestions regarding the early Pliocene climate and topography of eastern Oregon.

Age of the Flora

As previously stated, the age of the Dalles formation as indicated by the fossil flora is Lower Pliocene. Before considering in detail the evidence for this dating, it will be profitable to review the age determinations which have been made by other workers.

After four decades of field work in eastern Oregon, Condon made the following statement (1902, p. 143): "Years ago the writer designated the group of rocks to which this gray sandstone belongs as The Dalles Group and Pliocene." This age reference appears to have been based both on the position of the Dalles formation above the Columbia River basalt, and on comparison of its flora and fauna with those of the formations exposed in the John Day Basin.

Writing at approximately the same time, Knowlton referred the Dalles flora to the Upper Eocene (1902, p. 112). This determination was tentative, and based on the collection of specimens sent by Condon to Newberry many years before. The identifications by Newberry and Knowlton are given here, together with the names applied to these specimens in the present paper.

Newberry	*Knowlton*	*Chaney*
Acacia, or Cassia sp.	Acacia, or Cassia sp.	Amorpha condoni new species
Myrica diversifolia Lesquereux	Crataegus flavescens Newberry	Acer negundoides MacGinitie
Ulmus sp.	Carpinus grandis Unger	Specimen not seen

No specimens resembling either *Ulmus* or *Carpinus* are included in the Condon collection now at the New York Botanical Garden; it is possible, however, that a leaf of the type referred by us to *Ulmus californica* may originally have been included in this collection. Knowlton does not mention the *Cercis* leaves in the Condon collection, which are here referred to *C. buchananensis,* nor the fragments which may represent *Salix hesperia* as here determined. In referring this material to the Upper Eocene, Knowlton had in mind resemblances to species found in the Bridge Creek flora, termed Upper Clarno by him and considered to be of Upper Eocene age. The Bridge Creek flora has long been known to occur in the Lower John Day formation, the age of which is Upper Oligocene or Lower Miocene. Even though his references of specimens to *Carpinus grandis* and *Crataegus flavescens* (now *C. newberryi* Cockerell) were correct, these species are now known to range into the Upper Miocene or Mio-Pliocene deposits of western North America. As Condon realized (McCornack, 1928, p. 75), the reference of the Dalles formation to a horizon as low as

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Eocene is inconsistent with its position above the Columbia River basalt. It is clear that there is no basis, either floristic or stratigraphic, for placing the Dalles formation so far down in the Tertiary.

Previously the Condon collection had been doubtfully considered to be of Miocene age by Newberry (1898, p. 141), although he made no reference to it other than in a column heading in his table of distribution. It is not surprising that he felt uncertainty about an age assignment for the small collection he had available for study, especially in view of the limited information then available regarding other Tertiary floras in western North America.

On the basis of fragmentary mammalian remains, together with inferences from the stratigraphic position, structure, and lithology of the beds containing them, Buwalda and Moore have determined the age of the Dalles formation as Upper Miocene or Lower Pliocene (1930, pp. 16–18). They mention the similarity in structure and lithology between these deposits and the Ellensburg formation of Washington, which they state "is now known to be late Miocene or lower Pliocene." Preliminary studies of the first really adequate collections of plant fossils from the Ellensburg by George F. Beck and the writer indicate that this formation is of Lower Pliocene age. These collections, recently made by Beck, Leo Tyrrell, R. S. LaMotte, and the writer, will be considered below in comparison with the Dalles flora, and will be the subject of a paper in the near future.

In his discussion of the age of the Dalles formation, Piper (1932, p. 126) has stated: "It seems extremely probable that the three formations—The Dalles, Mascall, and Ellensburg—are approximately if not strictly correlative." A similar conclusion was reached by Collier (1914, p. 19). As stated above, and for reasons which will be discussed more fully below, the writer is in agreement with the correlation between the Dalles and Ellensburg formations. But the Mascall formation, in spite of structural and lithological similarities, has a flora so profoundly different as to indicate that it is older than the Dalles formation. A further basis for distinguishing the Mascall and Dalles formations at most outcrops is the predominantly finer texture, whiter color, and better induration of the volcanic sediments which make up the Mascall; this field distinction obviously has no bearing on the relative age of the two formations.

In Hodge's most recent discussion of the occurrence and age of the Dalles formation (1938, p. 869), he makes the following statement:

> That the Dalles formation is Pliocene, and may be earliest Pleistocene, in age is indicated by the following facts. A state of little erosion and much deformation occurred after the upper Miocene Mascall deposition and before the deposition of the Pliocene Rattlesnake formation, and a period of slight deformation and much erosion intervened between the Rattlesnake and the Dalles formations. Some fossils of the Dalles formation are Pliocene in age; others may be Pleistocene. The Dalles formation is poorly consolidated, and the lower beds have not been folded.

Several comments may be made on this statement: (1) The suggestion that the Dalles formation is younger than the Middle Pliocene Rattlesnake formation is not supported by field evidence, since no section is recorded in which they

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are in contact. Furthermore, all the available mammalian fossils indicate an age older than the well known fauna of the Rattlesnake. (2) The statement that some of the fossils (meaning vertebrates) of the Dalles formation may be Pleistocene is based on the erroneous conclusion that all the sediments in which vertebrate fossils occur are a part of the Dalles formation. Piper (1932, p. 131) has shown that they also occur in the older alluvium which lies in valleys eroded in the Dalles formation, and which is part of the Pleistocene terrace of the Columbia River. (3) The lower beds of the Dalles are considered by the writer to have been folded, as discussed on pages 289–290 of this chapter. (4) Hodge's opinion that the Dalles formation is of post-Miocene age is supported by the evidence of the fossil plants, as presented in this chapter.

An unpublished manuscript by Packard and Stirton describes the *Aelurodon* jaw and camel remains mentioned briefly in the introduction to this chapter. These specimens came from a road excavation 200 yards northwest of the plant locality on Chenoweth Creek, on the north side of the valley. At this point the section exposed along the old highway shows cross-bedded sands and ash, as well as coarser sediments in which the pebbles are prevailingly of volcanic origin. Above is a layer or lens of white ash 18 inches or more in thickness; Mr. Fauerso, who collected the mammalian remains here, and with whom the writer has visited the locality, states that they came from this ash layer, at a point slightly above the present level of the road and a short distance to the north. The structure and lithology of the beds here exposed indicate that the bone-bearing horizon has essentially the same stratigraphic position as the tuff lens in which the leaves occur on the south side of the creek. Attachment of white matrix to the *Aelurodon* jaw confirms its occurrence in the ash layer, and its excellent preservation indicates that it is contemporaneous with the enclosing sediments. Packard and Stirton compare this specimen with *A. saevus* (Leidy) of the late Upper Miocene, and with *A. inflatus* (VanderHoof and Gregory) from the late Lower Pliocene, and conclude that it and the fragmentary camel remains fall within this age range. VanderHoof and Gregory (1940, p. 146) have also studied the Dalles *Aelurodon,* which they refer to *A. saevus,* stating that it is larger than the type specimen from the Niobrara River fauna of Nebraska, and that it is of Pliocene age.

Turning to the testimony of the fossil plants, we may state with confidence that they represent an age younger than that of any Miocene flora recorded from the Columbia Plateau. The Miocene vegetation of this era is so well known, and the sequence of Tertiary floras so well established, that a sound basis is afforded for the reference of our material to the Pliocene. Table 29 shows the occurrence of 10 Dalles species recorded in other Tertiary floras of western North America; 2 of these, *Amorpha condoni* and *Pterocarya oregoniana,* are described and discussed for the first time in this volume. Of the seventeen floras with which the Dalles flora is compared in table 29, two, the Remington Hill and Troutdale, have not previously been discussed in print, and six, the Alturas, Alvord Creek, Table Mountain, Sonoma, Black Hawk Ranch, and Mulholland, are receiving much more adequate treatment in this volume than

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TABLE 29

OCCURRENCE OF DALLES SPECIES IN OTHER TERTIARY FLORAS

SPECIES	MIOCENE			TRANSITIONAL				PLIOCENE									
	LOWER	MIDDLE	UPPER					LOWER						MIDDLE			UPPER
	Eagle Creek	Latah	Mascall	Lower Idaho	Neroly	Remington Hill	Table Mountain	Ellensburg	Troutdale	Alvord Creek	Verdi	Ogallala	Black Hawk Ranch	Deschutes	Alturas	Mulholland	Sonoma
Acer negundoides	x	x	x	x	...	x	...	x	...	...	...	x	...	x	...	...	...
Amorpha condoni	...	...	...	...	...	...	...	...	x	x	...	...	...	...	...	...	x
Castanopsis sonomensis	...	...	o	...	...	...	...	...	...	...	...	...	...	...	...	...	x
Cercis buchananensis	...	...	...	...	...	...	x	x	...	...	...	...	...	...	...	...	...
Platanus dissecta	...	x	x	x	x	...	x	x	...	...	...	o	x	...	...	...	...
Pterocarya oregoniana	...	o	o	...	...	...	...	...	x	...	...	...	...	...	...	...	...
Quercus winstanleyi	...	o	o	o	...	x	...	x	x	...	...	...	...	...	...	...	...
Salix hesperia	...	x	x	x	x	x	...	x	...	...	...	...	x	...	...	x	...
Salix truckeana	...	...	...	...	...	...	...	...	...	...	x	...	...	...	x	...	...
Ulmus californica	o	o	o	x	...	x	x	x	x	...	...	o	x	...	o	...	...
Total in flora	1	3	3	4	2	4	3	6	4	1	1	1	3	1	1	1	2
Total in stage	1	3	3	6				9						3			2
Total in epoch	3			6				10									

x = identical species; o = related species.

in earlier publications; the Ellensburg is included in this table largely on the basis of unpublished data.

The totals at the bottom of table 29 show that there was a progressively larger representation of Dalles species from Lower Miocene to Pliocene, with the largest number recorded from beds of Lower Pliocene age. If the number of species involved were considered to be adequate, and if statistical analysis provided a complete and authoritative basis for correlation, the age of the Dalles flora would be established as Lower Pliocene without further comment. The methods of age determination now employed involve a much more critical discussion of plant distribution, both in time and in space, than can be shown in a table. Our conclusions as based on these methods, however, are in full accord with the statistical evidence of table 29.

Three of the 10 species with outside distribution are members of two well known Miocene floras, the Latah of Washington and Idaho, and the Mascall of Oregon with equivalent units in Nevada and Idaho. The Latah flora

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is considered to be of Middle Miocene age, and the Mascall represents the time interval from uppermost Middle Miocene to Upper, though probably not latest, Miocene. All the Dalles species with Miocene occurrence range up through transitional floras into the Pliocene. Obviously such long-ranging fossil species are less significant as age indicators than the many Miocene species which became extinct at the end of that epoch; among these may be mentioned *Carpinus grandis, Carya egregia, Fagus pacifica,* and *Ulmus speciosa,* whose modern equivalents live in eastern North America, and *Castanea orientalis, Fagus washoensis, Ginkgo adiantoides,* and *Tilia oregona,* whose modern equivalents live in eastern Asia.

In our discussion of the physical indications of the Dalles flora, we have indicated our belief that these extinctions at the close of the Miocene in western North America were the result of climatic changes involving reduced temperature and precipitation, the latter with seasonal restriction bringing dry summers. Such climatic changes are considered to have resulted in part from the building up of the Coast Ranges, Cascades, and Sierra Nevada to a height which made them effective barriers to the movement of moisture-bearing winds eastward (LaMotte, 1936, pp. 90–95); they were also related to modifications in atmospheric circulation resulting from altered temperatures on land and sea (MacGinitie, 1937, pp. 122–127). A considerable body of evidence places the date of mountain building along the Pacific coast as late Miocene to Pliocene, and the concurrent disappearance of many forest trees was inevitable. The survival of such species as *Acer negundoides, Platanus dissecta,* and *Salix hesperia* into the Pliocene seems to have been largely due to their greater hardiness. This is shared by their living equivalents now occupying stream borders and adjacent slopes in many parts of western North America, where the climate is more arid and seasonally restricted than that of Miocene and earlier Tertiary time. By contrast, the species becoming extinct at the close of the Miocene have surviving modern equivalents only in regions where rainfall is more uniformly distributed, and for the most part more adequate, than in western North America today; the forests of the eastern United States and eastern Asia include many genera which disappeared from the western United States during later Tertiary time, and particularly at the close of the Miocene epoch. Fossil species of such genera are obviously more valuable as stratigraphic indicators than the relatively hardy forms which survived into the Pliocene.

Four of the seventeen floras given in table 29, including the two described by Condit in this volume from the west slopes of the Sierra Nevada, are considered to be transitional in age between Miocene and Pliocene on the basis of present information. These include the 3 species with Miocene occurrence above mentioned, and 3 additional species known elsewhere only from Pliocene horizons, *Cercis buchananensis, Quercus winstanleyi,* and *Ulmus californica;* the latter is closely related to the Miocene *U. speciosa,* but has smaller leaves; *Q. winstanleyi* bears the same relation to the Miocene *Q. columbiana.* As might be expected from its closer proximity, the Lower Idaho flora from south-

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western Idaho contains more Dalles species than do those in California. This flora has a composition intermediate between the Miocene and Pliocene as developed elsewhere on the Columbia Plateau (Dorf, 1936, pp. 98–105). A Miocene aspect results from the occurrence in it of *Sequoia langsdorfii* in small numbers; of such members of the East American Element as *Ostrya oregoniana, Ptelea miocenica, Ulmus californica;* of several members of the East Asian Element, such as *Cercidiphyllum crenatum, Glyptostrobus europaeus,*[7] *Quercus simulata,* and *Trapa americana;*[8] and of *Cedrela oregoniana,*[9] a member of the Caribbean Element. More numerous in the Lower Idaho flora are evergreen oaks and conifers, which are suggestive of Pliocene age. The flora as a whole indicates conditions much drier than those typical of the Miocene, and the stratigraphic relations and associated vertebrate remains are also consistent with a Mio-Pliocene age assignment. Comparison with the Dalles flora shows *Acer negundoides, Platanus dissecta, Salix hesperia,*[10] and *Ulmus californica*[11] in common; these species are regularly present in other Pliocene floras of the western United States. Our flora lacks most of the broad-leafed deciduous genera which characterize the Lower Idaho, and appears to have lived under conditions of reduced summer rainfall. In its lack of conifers, live oaks, and other small-leafed evergreens, the Dalles flora suggests a different topographic setting, at a lower elevation where woody plants were largely confined to stream borders. At the higher altitudes occupied by the Lower Idaho flora, there was doubtless more summer rainfall even during the Dalles stage. Thus a facies difference as well as a discrepancy in time between the two floras is indicated, and we conclude that although the Dalles flora is definitely younger, the difference in composition is not so great as to indicate an age as late as Middle Pliocene.

The limited resemblance of the Dalles flora to the Neroly, of west-central California, partly explained by a slight difference in age, seems primarily the result of considerable differences in latitude and habitat. *Platanus dissecta,* the only species in common, is one of the dominant members of the Neroly flora, but is rare in the Dalles. The coastal location of the Neroly, with more moderate temperature and more uniform precipitation (Condit, 1938, pp. 234–242), and its latitude 8° south of The Dalles seem to provide an adequate basis for the difference between the two floras. Two other floras assigned to an age transitional between the Miocene and Pliocene are the Remington Hill and Table Mountain floras from the western slopes of the Sierra Nevada (see chaps. 2 and 3 of this volume). With these the Dalles flora has in common such Miocene species as *Acer negundoides, Platanus dissecta,* and *Salix hesperia,* together with *Quercus winstanleyi, Cercis buchananensis,* and *Ulmus californica,* which are typically Pliocene. In view of the differences in latitude and

[7] Not recorded by Dorf, but recently collected by Brown.
[8] Designated by Dorf as *T. prenatans.*
[9] Designated by Dorf as *Libocedrus* sp.
[10] Designated by Dorf as *Juglans hesperia.*
[11] Designated by Dorf as *U. speciosa* and *U. moorei.*

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age, this similarity is rather striking. It indicates that this late Tertiary forest had a north-south distribution approximating that of the Transition life zone at middle altitudes in the Sierra Nevada and Cascades today.

All the Dalles plants which have been assigned specific status have been recorded elsewhere from at least one Lower Pliocene horizon in the western United States; it is possible that the forms designated as *Prunus* sp. and *Vitis* sp. may represent species of these genera which are known from Pliocene floras in California, but their relationships are not conclusive. Among Lower Pliocene floras, the closest relationship is to the Ellensburg of eastern Washington; recently collected near Selah, about 80 miles northeast of The Dalles, this is the largest Lower Pliocene flora as yet known from the Columbia Plateau. An interior environment similar to that of the Dalles flora is indicated, although the Ellensburg appears to have been somewhat more humid, and possibly lived at a somewhat higher elevation. The occurrence of *Celtis kansana* and *Populus alexanderi* along with 6 of the Dalles species gives the Ellensburg a typically Pliocene aspect. Such characteristic species as *Acer negundoides, Cercis buchananensis,* and *Ulmus californica* are common to the Dalles and Ellensburg.

Less resemblance is apparent between the Dalles and Troutdale floras. Located in the lower Willamette Valley, 80 miles west of The Dalles, the Troutdale flora comes from a climatic province which has been distinct since Pliocene time, when the Cascade barrier first became effective. As will be more fully set forth in the following chapter, this flora reflects greater continuity of Miocene conditions into the Pliocene, as shown by its larger representation of the East American and East Asian Elements. The Dalles flora has 4 species in common with the Troutdale; *Quercus winstanleyi* and *Ulmus californica,* abundant in the latter, are only sparsely represented in the Dalles flora; *Amorpha condoni* is more numerous in the Dalles than in the Troutdale; *Pterocarya oregoniana* is rare in both. Clearly the two floras represent types of vegetation as different as those found on opposite sides of the Cascades today, although as now there are species in common.

Southward, the Alvord Creek flora of southeastern Oregon, studied by Axelrod (chap. 9), is largely montane in character, with only *Amorpha condoni* in common with the Dalles. Another Lower Pliocene flora of the interior is the Truckee from west-central Nevada, whose difference in composition and in environment is reflected by the occurrence of only 2 Dalles species, *Castanopsis sonomensis* and *Salix truckeana.* The southernmost known flora of this age from North America has been described from the Ogallala formation of western Oklahoma (Chaney and Elias, 1936); it has only *Acer negundoides* in common with the Dalles flora, although its species of elm and sycamore are closely related, or possibly identical. Also lying far to the south of The Dalles, and nearer to the coast, is the Black Hawk Ranch flora from west-central California, which is discussed in chapter 4. This is a flood-plain assemblage and includes 3 Dalles species, *Platanus dissecta, Salix hesperia,* and *Ulmus californica.*

Middle and Upper Pliocene floras are less well known in western North

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America than those from the Lower Pliocene; it is possible that closer relationships to the Dalles flora may be established when they have been more fully studied. The Deschutes flora, from an area 65 miles to the south, has been considered to be of Lower to Middle Pliocene age (Chaney, 1938*a*, pp. 204–212). There is only 1 species in common with the Dalles flora, *Acer negundoides*. The Deschutes flora appears to have lived at a higher elevation than the Dalles, on the slopes of a volcano. If the two floras had been contemporaneous, the Deschutes should have been the more mesic. Since it indicates a more arid environment than the Dalles flora, the Deschutes flora is considered to be somewhat younger and is now referred to the Middle Pliocene. Another adjacent flora of this age, from the Alturas formation of northeastern California, discussed in chapter 10, shows little resemblance to the Dalles flora, with a willow the only species in common. Except for *Ulmus moragensis* in the Alturas flora, the East American and East Asian Elements are missing from the Deschutes and Alturas as now known, a fact which is consistent with their younger age and more arid environments. Resemblance of the Dalles flora to the Mulholland and others from the Middle Pliocene of California is slight.

The Sonoma flora from the Upper Pliocene of west-central California, discussed in chapter 7, contains only 2 of the Dalles species, *Amorpha condoni* and *Castanopsis sonomensis,* both of which have modern equivalents in this part of California. Most of the Sonoma flora is of a coastal type, and its lack of similarity to the inland Dalles flora is to be expected.

Summarizing the age indications of the Dalles flora, it is referred to the Lower Pliocene on the basis of the following evidence:

1. Stratigraphic evidence: The Dalles formation lies upon the Columbia River basalt, and is therefore known to be younger than Middle Miocene. If, as has been suggested, the flows at the top of certain sections of the Columbia River basalt are as young as Upper Miocene or even Lower Pliocene, the older limits of age of the Dalles formation are further restricted.

2. Mammalian evidence: The genus *Aelurodon,* represented by our most complete vertebrate specimen, has a time range from late Upper Miocene through Lower Pliocene. The two species to which the Dalles jaw is related are *A. saevus* from the uppermost Miocene Niobrara River fauna of Nebraska, and *A. inflatus* from the Lower Pliocene at Big Spring Canyon, South Dakota. Camel remains and a horse tooth resembling *Hipparion condoni* likewise indicate Lower Pliocene or possibly Upper Miocene age.

3. Plant evidence: All 10 species with outside distribution have been recorded from the Lower Pliocene. Three species range down into the Upper and Middle Miocene, and 2 into the Lower Miocene. Three species range up into the Middle Pliocene, and 2 into the Upper Pliocene. More significant than these numerical relationships is the low representation of typical Miocene species in the Dalles formation. The dominance of trees and shrubs whose modern equivalents occupy riparian habitats in regions with climatic extremes serves to emphasize the difference between the Dalles flora and the well

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known Miocene vegetation of the Columbia Plateau. The environment indicated by *Acer negundoides* and its associates in the Dalles flora is of the cool, semiarid type which characterized the post-Miocene floras of the continental interior in western North America. The presence of a few Miocene relicts, however, including members of the East American and East Asian Elements, seems definitely to indicate an age older than Middle Pliocene, since these elements are not known to have survived beyond Lower Pliocene time at interior localities.

4. With the evidence of the plants indicating its post-Miocene age, and with the mammalian and plant evidence setting its age as older than Middle Pliocene, the Lower Pliocene age of the fossil-bearing lower part of the Dalles formation is well established.

5. The upper part of the Dalles formation is not known to contain fossils, and its age is therefore not directly indicated. Pyroclastic deposits of this type are ordinarily considered to accumulate rapidly, and the age of the whole formation may well be Lower Pliocene. Favoring the reference of the upper, nonfossiliferous part of the Dalles formation to the Middle Pliocene are the following considerations: (*a*) The essentially horizontal position of the beds comprising the upper part of the formation suggests that they may be younger than the lower, folded part of the Dalles formation; (*b*) the Deschutes formation, lying to the south, has a similar horizontal position above folded flows of Columbia River basalt; though the Deschutes flora is too small to afford a wholly satisfactory basis for comparison, it appears to be younger than the Dalles flora and is now considered to be of Middle Pliocene age; if the Deschutes formation is the equivalent of the upper part of the Dalles formation, the latter seems referable to the Middle Pliocene. With the discovery of plant fossils or the remains of mammals in the upper part of the Dalles formation it will be possible to determine its age with relation to the lower part, and a better basis will be afforded for correlation with the Deschutes formation.

Summary

The Dalles flora, comprising 12 species, occurs in fine tuffs in the basal part of the Dalles formation. These andesitic pyroclastics overlie the Columbia River basalt on the east side of the Cascades in northern Oregon, and are considered the equivalent of the Troutdale formation on the west slope of the range. Members of the East American and East Asian Elements include only a few typical Miocene species; for the most part they represent hardy types which have also survived to the present along streams in semiarid parts of the western United States, and which are more readily referable to the West American Element. Such plants are characteristic of the Pliocene in this region, and indicate precipitation largely restricted to the winter months. Assignment of the Dalles formation to a Lower Pliocene age is based on this mingling of a residue of Miocene species with typical Pliocene species, and on the pre-Middle Pliocene indications of associated vertebrate remains.

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SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA

Class ANGIOSPERMAE

Subclass DICOTYLEDONES

Family SALICACEAE

Salix hesperia (Knowlton) Condit

(Plate 53, figure 1)

Salix hesperia (Knowlton) Condit, Carnegie Inst. Wash. Pub. 553, pp. 41–42, pl. 4, fig. 7, 1944 (see synonymy and discussion).

Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

The Dalles specimens resemble the leaves of *Salix lasiandra* Bentham, a relationship which Berry has pointed out for the Latah material. Large-leafed willows of this modern species are generally referred to the variety *lancifolia* Bebb, which ranges from California through Oregon to Alaska. Smaller fossil leaves also fall within the limits of size range of *S. lasiandra*, and are referred to *S. hesperia* in spite of their rather marked variation in shape. The modern *S. lasiandra* is a common flood-plain species along the Columbia River and its tributaries.

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2786, 2786*a* (counterpart).

Salix truckeana new species

(Plate 52, figures 2–6)

Description. Leaves long lanceolate, 5.0 to 10.0 cm. long and 0.4 to 1.1 cm. wide; tip in all cases missing; base rounded cuneate; petiole stout, 0.4 to 0.6 cm. long; midrib rather heavy at base of leaf; long, alternate secondaries leaving midrib at angles of from 50° to 80°, curving upward to the outer third of the blade, then extending nearly parallel to the midrib, each vein running along outside the one above; tertiaries an irregular, angular mesh, becoming percurrent in the outer part of the blade, forming many connections between the long secondaries; teeth small, serrate, evenly and rather widely spaced, inconspicuous in the basal part of the leaf; texture thin to firm.

Discussion. Several leaves of this type have also been collected at the Verdi locality of the Truckee formation in west-central Nevada; this formation is considered by Axelrod to be of Lower Pliocene age. Leaves similar in shape and only slightly smaller than the largest Dalles specimen are included in the original collection from the Alturas formation, of Middle Pliocene age.

Salix truckeana shows a close resemblance to the living *S. gooddingii* Ball. Related willows of the *nigra* type are found today along the streams in the immediate vicinity of the fossil localities.

Occurrence. Chenoweth Creek, loc. 3941; Verdi, Nevada, loc. 102.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2787, 2788 (loc. 3941), 1991, 1992, 1993, 1994 (loc. 102).

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Family JUGLANDACEAE

Pterocarya oregoniana Chaney

Pterocarya oregoniana Chaney, Carnegie Inst. Wash. Pub. 553, pp. 341–342, pl. 57, fig. 6; pl. 58, figs. 1, 4, 1944.

Only fragmentary leaflets are available in the Dalles collections. The description of this species is included in the chapter which follows, since the Troutdale specimens are well preserved and more numerous.

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2800.

Family FAGACEAE

Castanopsis sonomensis Axelrod

Castanopsis sonomensis Axelrod, Carnegie Inst. Wash. Pub. 553, pp. 196–197, 1944 (see synonymy).

This species differs from the widely distributed *Castanopsis perplexa* (Knowlton) Brown of the Miocene in having more slender leaves, with their apices long pointed instead of obtuse rounded. *Castanopsis perplexa,* like its modern equivalent, *C. sempervirens* Dudley, seems to have been largely confined to the interior. *Castanopsis sonomensis* and its modern equivalent, *C. chrysophylla* A. DeCandolle, are primarily coastal species. The fossil species has been previously reported only from western California (see pp. 196–197 of this volume). *Castanopsis chrysophylla* ranges along the west slopes of the Cascades from southern Washington through Oregon; in California it reaches its best development in the coastal forests of Humboldt and Mendocino counties, extending eastward through the Coast Ranges. Of particular significance to the present study are the records of its presence (Sudworth, 1908, pp. 273–274) in southwestern Washington at "Moffat's Springs, Skamania County, the only station now known," and at "Dalles of Columbia." It is so rare in the Dalles region that the writer has never seen it there. The Dalles record of *C. sonomensis* indicates that during Pliocene time a coastal species of chinquapin extended inland from the coast along the larger valleys as its modern equivalent does today.

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2789.

Quercus winstanleyi Chaney

(Plate 52, figure 1)

Quercus winstanleyi Chaney, Carnegie Inst. Wash. Pub. 553, pp. 342–345, pl. 60, figs. 1, 3–5; pl. 61, figs. 1, 2, 4; pl. 62, fig. 2, 1944.

This species is abundantly represented in the Troutdale flora. Its description and the discussion of its relationships are therefore included in the chapter which follows. The oak leaves from the Dalles collections are fragmentary and few in number.

Occurrence. Chenoweth Creek, loc. 3941; Condon loc.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2790 (specimen missing).

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Family ULMACEAE

Ulmus californica Lesquereux

Ulmus californica Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. 7*a*, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 46, pl. 8, fig. 4, 1944 (see synonymy).

The problem involved in the specific designation of these Lower Pliocene elm leaves is considered in the discussion of the Troutdale flora, in the chapter which follows. The leaves of *Ulmus californica* in the Dalles and Troutdale floras average smaller than those of *U. speciosa* Newberry, which is widespread in Miocene and Oligocene floras of the Columbia Plateau.

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2791, 2792, 2793.

Family PLATANACEAE

Platanus dissecta Lesquereux

Platanus dissecta Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 13, pl. 7, fig. 12; pl. 10, figs. 4, 5, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, pp. 80–81, pl. 15, figs. 1, 4, 1944 (see synonymy).

The scarcity and fragmentary preservation of sycamore leaves in the Dalles formation are in striking contrast with their common occurrence in many of the Miocene floras of the Columbia Plateau, and in the Ellensburg flora of Pliocene age. The Dalles specimens are incomplete, but their margins and shape are more suggestive of *Platanus dissecta* than of other Tertiary species. Their reference to this species is further supported by its abundant occurrence in the near-by Ellensburg flora, to which the Dalles flora shows many close relationships.

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2794, 2794*a* (counterpart).

Family ROSACEAE

Prunus sp.

Although leaves of *Prunus* are of common occurrence in Pliocene floras of western North America, and are numerous at the Troutdale locality on the west slope of the Cascades, none has been found as yet in the Dalles formation. The only record of this genus is wood found on the north slope of the valley of Chenoweth Creek, opposite the principal leaf locality. The specimens indicate the presence of a medium-sized cherry tree. The writer is indebted to Professor George F. Beck, of Central Washington College of Education, for the determination of this material.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 1699.

Family LEGUMINOSAE

Amorpha condoni new species

(Plate 51, figures 2–4)

The specimens from the Dalles formation were collected by Thomas Condon, in whose memory the specific name is assigned. Unlike that at the Chenoweth locality, the matrix in which all these specimens occur is a coarse sandstone, in which the finer details of nervation are not preserved. Fortunately additional leaflets have recently

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been collected at the Camp Collins locality of the Troutdale formation. The following description is based on the material from both localities.

Description. Leaves compound, a stout rachis with leaflets apparently opposite, in the present specimens with a maximum of 7 leaflets on one side of the rachis, short-petiolate, with the maximum observed petiolule 1.5 mm. long. Leaflets ovate, oval, or lanceolate, cuneately asymmetrical at the base with the distal side commonly more broadly rounded, apex narrowly rounded to acute, or bluntly rounded and emarginate; length 8 to 30 mm., width 5 to 13 mm.; midrib slender; secondaries subopposite, branching acutely near the base, at nearly right angles in the distal two-thirds of the broader leaflets, camptodrome; finer nervation obscure; margin entire, apparently recurved in some cases; texture firm to coriaceous.

Discussion. In 3 specimens the leaflets are attached to the rachis, in numbers of 4, 4, and 9. The discovery of these specimens greatly impressed Condon, who called them acacia in his notes and letters; he mentions a branch "carrying three or four large thorns" (1902, p. 145). The whereabouts of this specimen is unknown, but if our determination of the foliage as *Amorpha* is correct, it could not have belonged to the same plant, for this genus is not characterized by large thorns.

Not including *Amorpha utensis* Cockerell, from the Green River formation of Colorado, which seems too fragmentary to be certainly determinable, the only other Tertiary record of this genus is from the Kinnick formation of California (Axelrod, 1939, pp. 111–112, pl. 9, figs. 2–4). This Miocene species, *A. oblongifolia,* has leaflets with broader tips, but is clearly related to *A. condoni.* Both these species show a resemblance to *A. californica* Nuttall, now occupying coastal mountain slopes from central to southern California; the Oregon species seems also to be related to *A. fruticosa* Linnaeus, which is widely distributed from California eastward to Pennsylvania and Florida.

Several other leaflets referred to genera of the Leguminosae have been recorded from Tertiary deposits. *Robinia brittoni* Cockerell, from the Florissant flora of Colorado (Knowlton, 1916, p. 277, pl. 24, fig. 2), has subopposite leaflets whose shape and nervation resemble those of *A. condoni;* this flora is now considered by MacGinitie to be of Oligocene age. *Sophora spokanensis* Knowlton has leaflets of the same general shape, but somewhat larger and with heavier midribs; Berry (1929, p. 253) has suggested that this species may better be referred to *Robinia.* The size and shape of the leaflets of *Gymnocladus miochinensis* Hu and Chaney (1938, p. 52, pl. 27, figs. 4, 7) are in general similar to those of *A. condoni;* this Upper Miocene species from Shantung, China, differs in details of nervation and in the apparently alternate attachment of its leaflets.

Occurrence. Condon loc., Group C near The Dalles; Camp Collins, loc. P3922.

Collection. N. Y. Bot. Garden, cotypes, nos. 30,002, 30,003, 30,004.

Cercis buchananensis Condit

(Plate 51, figure 1)

Cercis buchananensis Condit, Carnegie Inst. Wash. Pub. 553, pp. 82–83, pl. 17, figs. 1, 3, 6, 1944.

The well preserved leaves of this species described by Condit from Table Mountain, California, are somewhat smaller than the leaves collected in the Dalles formation. Recent collections from the Ellensburg formation include numerous large redbud leaves, with some ranging down to the size of the California specimens. This variation in size corresponds to that in related living species, and is also closely

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paralleled by the leaves of *Cercis miochinensis* Hu and Chaney, from the Upper Miocene of Shantung. The large, cordate fossil leaves show closest resemblance to *C. canadensis* Linnaeus, of the eastern United States and Canada, and to *C. chinensis* Bunge of China. The rounded tips of the fossils also suggest relationship to the western *C. occidentalis* Torrey.

Reliable records of *Cercis* are comparatively rare in the Tertiary of the western United States. Leaves which have been assigned to this genus by Berry (1934, pp. 114–116, pl. 21, fig. 1; pl. 22; pl. 23, figs. 3–6) and by Brown (1937, pp. 177–178, pl. 54, figs. 8, 9) differ in essential respects from those of any living *Cercis* leaves; their association with *Cercis*-like pods is noted, but the pods also differ from those of living species. The relations of this material to *Cercis* will be more fully considered in a report on the Miocene floras of Oregon now in progress. The suggestion may be made that the specimens from the Latah formation of Washington and Idaho might better be placed in a form genus than assigned to a modern genus whose leaves and pods indicate such marked differences. Possibly a new genus of the Leguminosae may be established to include all or part of this material, and to emphasize the fact that plants with characters unlike those of any known redbud of today lived in western North America during the Miocene epoch.

Occurrence. Chenoweth Creek, loc. 3941; Condon loc., Group C near The Dalles.

Collection. N. Y. Bot. Garden, plesiotype, no. 30,001.

Family ACERACEAE

Acer negundoides MacGinitie

(Plate 53, figures 2, 4)

Acer negundoides MacGinitie, Carnegie Inst. Wash. Pub. 416, II, p. 62, pl. 11, figs. 2, 3, 1933.

Condit, Carnegie Inst. Wash. Pub. 553, p. 50, 1944 (see synonymy).

Although fruits of this Tertiary box elder are relatively common in Miocene and Pliocene deposits, this is the first flora in which leaflets are abundant. Even here their preservation is not good, which suggests that one of the reasons for rarity or absence of foliage units in the fossil record may be their fragility. The abundance of the remains of *Acer negundoides* in the Dalles formation is interpreted to indicate that it was a dominant tree along the stream which deposited these volcanic sediments. Proximity of box elder trees to sites of deposition is substantiated by the specimen with several associated fruits, shown on plate 53, figure 2, for it seems probable that this raceme dropped directly into the stream from the tree on which it grew. Dissociated samaras are also fairly numerous. Only 2 specimens show leaflets attached to the rachis.

Occurrence. Chenoweth Creek, loc. 3941; Condon loc., Group C near The Dalles.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2796, 2798; nos. 2795, 2797; N. Y. Bot. Garden, no. 30,005.

Family VITACEAE

Vitis sp.

(Plate 53, figure 3)

Fossil representatives of the genus *Vitis* are uncommon in the Tertiary of western North America. This need not indicate that the grape was rare, for its climbing

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habit may not have been readily conducive to the entrance of its leaves into the fossil record.

The single incomplete leaf included in the Dalles collections has the general appearance of *V. washingtonensis* (Knowlton) Brown (1937*a*, p. 181, pl. 56, figs. 5, 6; pl. 57, figs. 1, 2) from the Middle Miocene Latah flora of Washington, and from the White Bird flora of the same age of Idaho. The status of this species is not altogether satisfactory, since the marginal nervation of several specimens placed in synonymy by Brown is characteristic neither of *Vitis* nor of the Vitaceae. A further difficulty in referring the Dalles leaf to *V. washingtonensis* is its much smaller size as compared with the figured leaves of this species. In view of the inadequacy of our material, it is here referred only to the genus *Vitis*, whose modern leaves it closely resembles in the nervation characters of its base.

In size and general appearance, the Dalles specimen shows a marked similarity to a leaf recently collected by Axelrod from Upper Miocene deposits in southern California; only a preliminary statement has as yet been issued on this flora, which is termed the Mint Canyon flora (Axelrod, 1940*c*). Even more like our specimen is a fragment figured only as "Leaf associated with *Cercis* sp." from the Latah flora of Idaho (Ashlee, 1932, pl. 1, fig. 7A).

Occurrence. Chenoweth Creek, loc. 3941.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2799.

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PLATES 49—53

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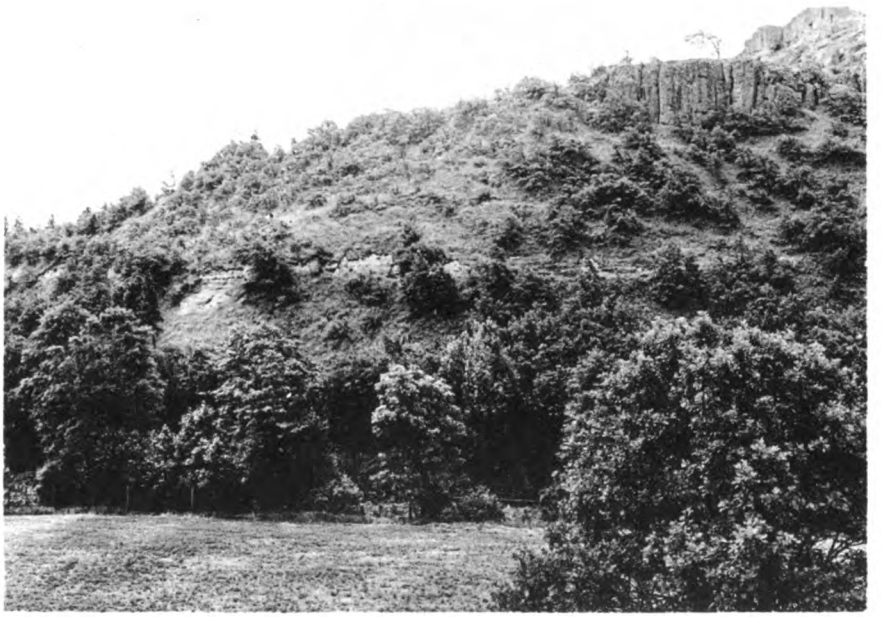

FIG. 1. Dalles formation exposed on south bank of Chenoweth Creek, 2½ miles northwest of The Dalles, Oregon.

FIG. 2. Locality 3941, on south bank of Chenoweth Creek. Leaf-bearing horizon in lower center of picture.

DALLES LOCALITY

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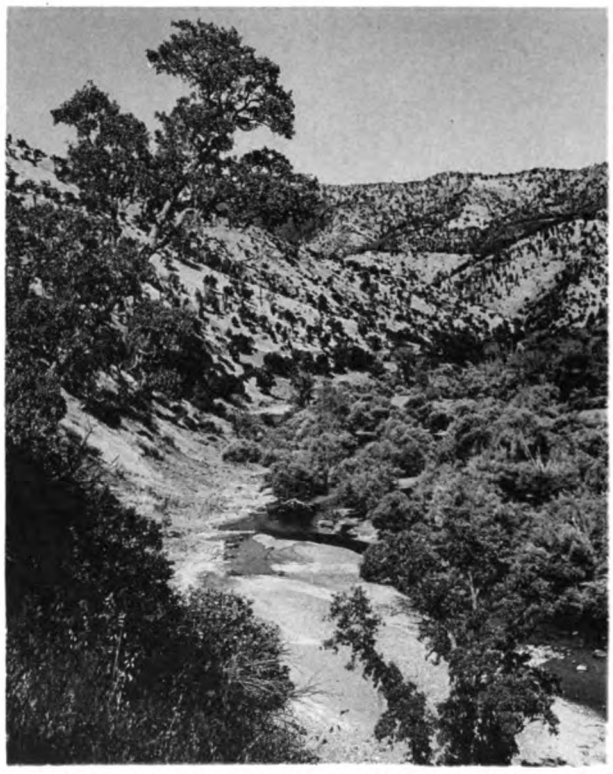

FIG. 1. Valley of Putah Creek, 4 miles west of Winters, California. Valley oak and pine on slopes; box elder, willow, and other riparian species along the creek.

FIG. 2. Valley of Putah Creek, 15 miles northwest of Winters. Redbud, willow, and valley oaks on the flood plain.

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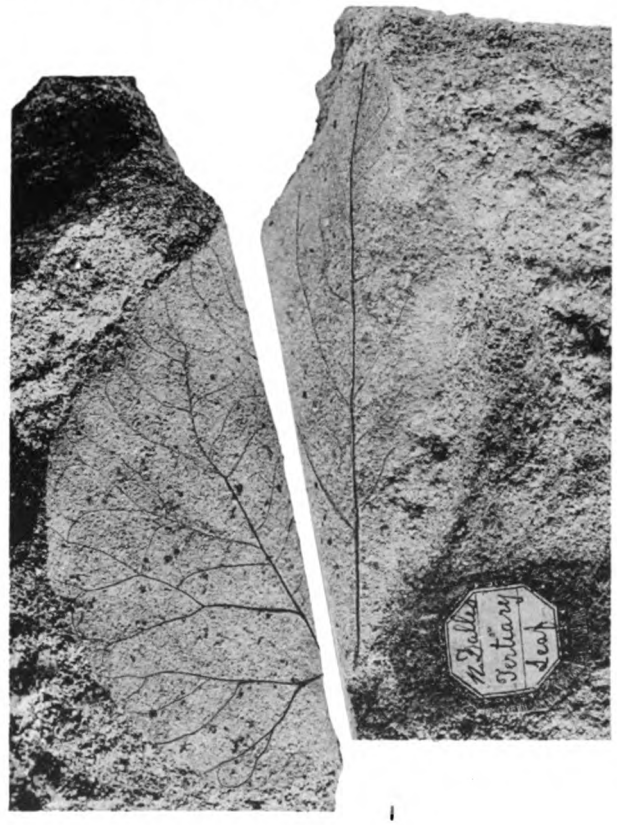

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DALLES FOSSILS

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FIG. 1. *Cercis buchananensis* Condit. Plesiotype. N. Y. Bot. Garden, no. 30,001. Two views of the specimen, which is curled around the rock 319

FIGS. 2–4. *Amorpha condoni* Chaney. Cotypes. N. Y. Bot. Garden, nos. 30,004, 30,003, 30,002 318

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PLATE 52

DALLES FOSSILS

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FIG. 1. *Quercus winstanleyi* Chaney. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2790 317

FIGS. 2–4. *Salix truckeana* Chaney. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1992, 1993, 1991. From locality 102 316

FIGS. 5, 6. *Salix truckeana* Chaney. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2787, 2788. From locality 3941. 316

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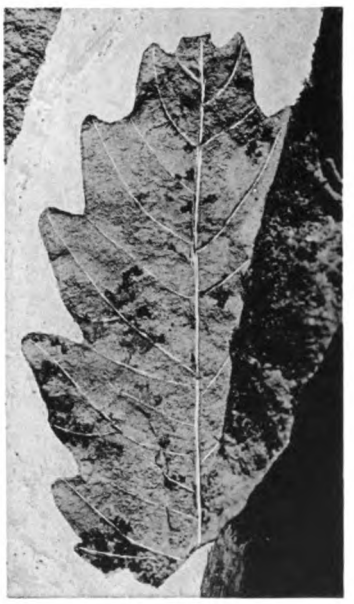

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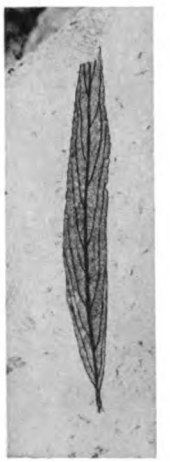

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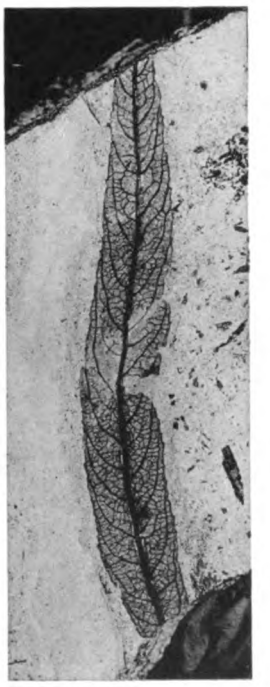

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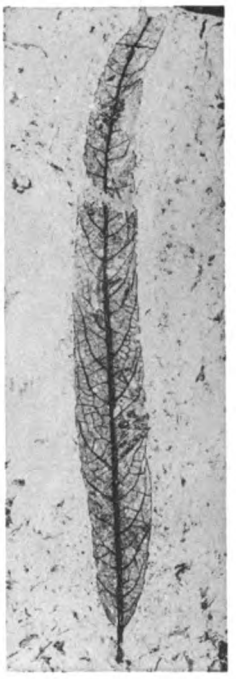

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PLATE 53

Dalles fossils

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Fig. 1. *Salix hesperia* (Knowlton) Condit. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2786 316

Figs. 2, 4. *Acer negundoides* MacGinitie. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2798, 2796 320

Fig. 3. *Vitis* sp. U. C. Mus. Pal., Paleobot. Ser., no. 2799 320

Ser., nos. 2136, 2137 261

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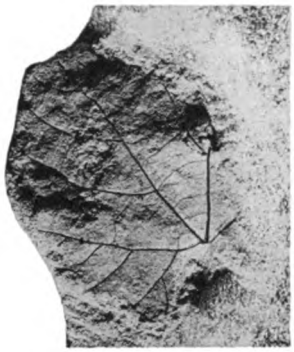

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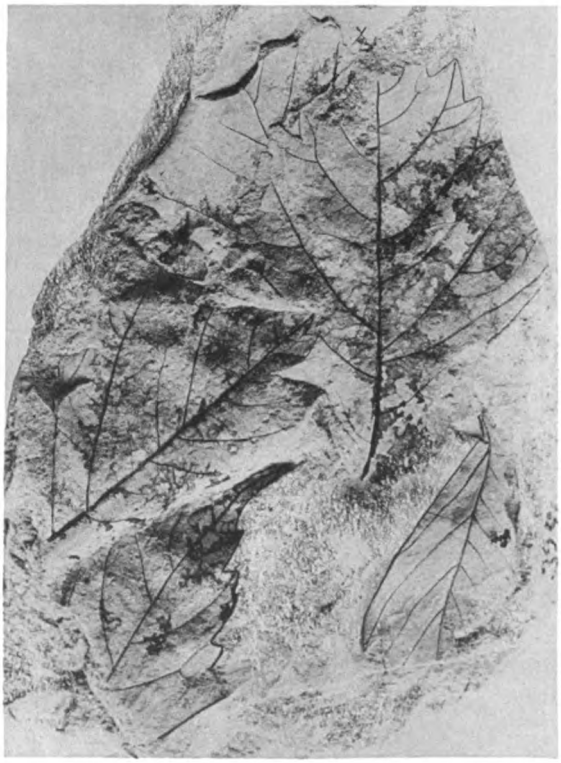

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12

The Troutdale Flora

RALPH W. CHANEY

Introduction

Since early pioneer days the people of Oregon have shown an enthusiastic interest in geology and paleontology. Such an interest is natural in a region of rocky shores, young volcanic mountains, and multi-colored hills exposing abundant records of past life. It was to be expected that the miners who came in search of gold might develop a lasting regard for the rocks in which they found it. But factors deeper-lying than topography and natural resources have been responsible for the maintenance of this active interest in earth history for more than three-quarters of a century. It began with the arrival of Thomas Condon at The Dalles in the sixties, and was continued during his long career of teaching and lecturing. In later years it has been sustained and extended by Condon's successors in the institutions of higher learning in the state. The Geological Society of the Oregon Country, an active organization founded in 1935, counts among its members men who felt the direct inspiration of Condon's instruction, and many later arrivals who have inherited the traditions of his vigorous inquiry and sound interpretation.

During my first season in Oregon, I had the good fortune to meet one of Condon's former students, J. B. Winstanley, then a resident of Portland. With him I worked my way through the heavy undergrowth of Buck Creek to visit the principal fossil plant locality of the Troutdale formation. He turned over to me his collections from this and other localities, and during the years of his residence in Oregon gave other valued assistance. It is a pleasure to acknowledge his cooperation in the study of the Troutdale flora, and to mention that his lifelong interest in paleontology had its origin in the classroom of Oregon's first geologist.

The Troutdale formation was named by Hodge in 1938 (p. 873) for "a great piedmont fan deposit lying on the west side of the Cascade zone." He discussed its lithology, structure, and relations to similar deposits across the Cascades to the east, concluding that it is the equivalent in part of the Dalles formation, representing "the closing stage of Dalles time." Its age he has placed as "probably earliest Pleistocene."

This age reference is in accord with the conclusions of Williams (1916) and Bretz (1917), who were the first to study the gravels extending across the Cascade Range along the Columbia Gorge. Their incorrect correlation of these gravels with the Pleistocene Satsop formation of western Washington resulted in a dating far too young both for the gravels and for the Cascade orogeny. Fossil plants representing only a small part of the material now available were

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also used as evidence of Pleistocene age. As stated in the section on "Age of the flora," the Troutdale flora as now known is considered to be of Lower Pliocene age.

Buwalda and Moore have pointed out (1927, 1930) the reasons for assigning a "Middle Neocene" age to the Hood River conglomerate. This formation is a part of the "Satsop" formation as discussed by Williams and Bretz, and has recently been extended into eastern Washington by Warren (1941). All these authors are in agreement that the Hood River, Dalles, and Ellensburg formations are not younger than Lower Pliocene and may be as old as Upper Miocene. Their papers have added much valuable information regarding the later Tertiary history of the Columbia Plateau, and the relations of the volcanic and sedimentary rocks there exposed.

In 1916 the writer first studied the Troutdale formation under the direction of Bretz; the party was guided to the fossil-plant locality on Buck Creek by Winstanley, and made collections which have since been augmented with the field assistance of R. J. Russell, B. B. Wilder, E. Richardson, and R. C. Treasher. Treasher discovered the locality above Camp Collins, and with his associate Lloyd Ruff, of the Department of Geology and Mineral Industries of the State of Oregon, has in various ways assisted our study of the Troutdale formation.

Geologic Occurrence

No discussion of the Troutdale formation as a whole will be attempted in this report. Widely distributed in the area from Portland east and southeast to the Cascades, it represents the channel and alluvial-fan deposition of streams which flowed down the seaward slopes of late Tertiary volcanoes. The Troutdale is here considered to be of essentially the same age as the Dalles and Ellensburg formations, which were deposited on the inland slopes of these volcanoes during Lower Pliocene time. In texture the volcanic sediments of the Troutdale formation range from clays, fine sands, and grits to conglomerates with well rounded pebbles and cobbles. Fine-grained pyroclastic materials are less conspicuous than in the Dalles formation, as is consistent with the deposition of the Troutdale formation on the windward rather than the leeward side of the Tertiary volcanoes. Coarser materials are largely of basalt, although quartzite pebbles are locally common. The conglomerates of the Troutdale differ from those of the Dalles formation in containing better-rounded material, and in predominance of basalt. Like the Dalles, these sediments are locally well indurated and may occur in well defined lenses (pl. 55, fig. 1). Plant fossils are known to occur in fine volcanic clays at two localities in the valley of the Sandy River.

No complete section of the Troutdale formation is exposed, but Treasher estimates its maximum thickness at from 1000 to 1200 feet, and states that its observed thickness at any one point is only half this amount (oral communication, 1941). This is in accord with observations by Bretz (1917, p. 451). Though its structure is essentially horizontal in the valley of the Sandy River, Treasher (1942, p. 9) states that it is deformed with the Columbia River basalt near

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Council Crest. The writer's observations near Crown Point lead him to agree with Bretz (1917, p. 453, fig. 2) that it is folded with the Columbia River basalt across the Cascade Range. Consistent with this interpretation, and with the suggestion made by Bretz (*ibid.*, p. 454) that the Dalles formation is the equivalent of the Troutdale (his Satsop), is the close relationship between the Dalles and Troutdale floras.

The characteristic topography developed on the Troutdale surface serves as an indicator of its presence over large areas in the lower valley of the Willamette River and eastward. This topography has been developed to maturity (see Bretz, 1917, p. 451), with an average relief of several hundred feet. Treasher has pointed out that the basic flows which he terms the Boring lava, and which he considers probably equivalent in age to the "Cascan formation of Hodge," cap eroded Troutdale hills. The Boring lava also lies in valleys of this surface, as does the Boring agglomerate, comprising mudflows and volcanic sediments. He tentatively refers these two later formations to a late Pliocene or early Pleistocene age (1942, pp. 9–10).

The localities where plant fossils have been collected are in Multnomah County, at the northern edge of the Boring Quadrangle, about 2 miles apart. Following are their geographic locations, the sections exposed, and the lists of species collected:

Buck Creek locality (*Univ. Calif. loc.* 5). (See plate 54.) South bank of Buck Creek, ½ mile east of the road from Corbett to Bull Run, 4½ miles north of Bull Run in the extreme northeast corner of the Boring Quadrangle, at an elevation of approximately 300 feet. This is in the NE. ¼ NE. ¼ Sec. 11, T. 1 S., R. 4 E.

At the point of the fossil occurrence, a ledge outcrops for several hundred feet along the south side of the valley, exposing the following section:

	Thickness	
	Feet	*Inches*
Grit and sandstone with scattered pebbles	15	
Fine, tuffaceous sandstone with a few leaf impressions	4	
Fine ash with abundant leaf impressions		3–6
Gray to yellow tuffaceous sandstone to bottom	15	
Total	34	3–6

The sandy conglomerate at the top of the section contains only scattered pebbles and cobbles of basalt and quartzite. The upper 10 feet is a yellow grit similar to that exposed at various points along the gorge of the Columbia River; the lower 5 feet is gray sandstone. There is an irregular contact, apparently representing an erosion surface, between the 4-foot lens of tuffaceous sandstone and the underlying seam of leaf-bearing ash. Most of the leaves occur along this contact. Similar sediments are exposed downstream on the south side, but no plants have been collected, nor has any ash been noted. Near the crossing of the Bull Run road, coarse cobble conglomerate outcrops about 100 feet above the section containing plant fossils and for several miles southward; this may

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represent post-Troutdale outwash. Fragments of lava on the south slope of Buck Creek are interpreted as probably derived from the Boring lava.

Following is the list of species of the Buck Creek florule:

Abies axelrodi
Acer sp.
Chamaecyparis gracilis
Cornus ovalis
Cyperacites sp.
Fraxinus caudata
Liquidambar pachyphyllum
Phyllites plinerva
Prunus treasheri
Quercus winstanleyi
Salix wildcatensis
Sequoia langsdorfii
Umbellularia salicifolia

Camp Collins locality (*Univ. Calif. loc. P3922*). (See pl. 55, fig. 2.) South bank of Hossner road about 25 feet above the lower terrace of Sandy River at Camp Collins, at an elevation of approximately 125 feet. This is in the NE. ¼ NE. ¼ Sec. 9, and in the NW. ¼ NW. ¼ Sec. 10, T. 1 S., R. 4 E., of the Boring Quadrangle.

The following section along the road is based on field notes supplied by Treasher, who discovered the occurrence of plant fossils here:

	Thickness in feet
Glacial outwash, with well rounded lava boulders	32
Brown, cross-bedded sands representing the upper part of the Troutdale formation	6
Basaltic sand with boulders; clay at top	19
Basaltic sand, bluish and reddish banded	7
Clay	16
Massive basaltic sand, well indurated, grading into clay above	10
Indurated tuff grading into indurated felsite sand; two leaf zones, the lower with fragments, the upper with complete specimens mostly along one bedding plane	2
Fine quartzose sand grading up into clay	22
Conglomerate with rounded pebbles 1 to 3 inches in diameter; base not exposed	4
Lower terrace of the Sandy River	
Total	118

Leaf impressions are largely limited to an ashy parting in the layer of sandy tuff. They are not horizontally oriented as in the tuffs on Buck Creek. Following is the list of species collected:

Amorpha condoni
Diospyros andersonae
Fraxinus caudata
Pterocarya oregoniana
Quercus winstanleyi
Rhamnus troutdalensis
Salix wildcatensis
Ulmus californica
Zelkova oregoniana

It will be noted that the lists from the Buck Creek and Camp Collins localities contain few species in common. The significance of these florule differences

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will be considered in the section on "Composition and physical indications."

We shall discuss in the section on "Age of the flora" our reasons for placing the Troutdale formation in the Lower Pliocene, rather than in the Pleistocene as indicated by Bretz and Williams, or in the Middle Pliocene to Pleistocene as suggested by Hodge. For the purposes of the present discussion, it need only be pointed out that the Troutdale formation lies upon the Columbia River lava and is therefore post-Middle Miocene (possibly post-Miocene) in age; and that it is overlain by the Boring lava and is therefore older than the Upper Pliocene or Lower Pleistocene.

Composition and Physical Indications

The Troutdale flora as now known comprises 19 species, including 3 conifers, a doubtfully assigned monocotyledon, and 15 dicotyledons. Except the Ulmaceae, with *Ulmus* and *Zelkova,* the 17 families are each represented by a single genus and species. This is in striking contrast with most of the Middle and Lower Tertiary floras of western North America, in which such common families as Betulaceae, Fagaceae, and Lauraceae are usually represented by several genera, each of which may include several species.

Systematic List of Species

Spermatophyta
- Gymnospermae
  - Coniferales
    - Pinaceae
      - Abies axelrodi new species
    - Taxodiaceae
      - Sequoia langsdorfii (Brongniart) Heer
    - Cupressaceae
      - Chamaecyparis gracilis Condit
- Angiospermae
  - Monocotyledones
    - Glumiflorae
      - Cyperaceae
        - Cyperacites sp.
  - Dicotyledones
    - Salicales
      - Salicaceae
        - Salix wildcatensis Axelrod
    - Juglandales
      - Juglandaceae
        - Pterocarya oregoniana new species
    - Fagales
      - Fagaceae
        - Quercus winstanleyi new species
    - Urticales
      - Ulmaceae
        - Ulmus californica Lesquereux
        - Zelkova oregoniana (Knowlton) Brown

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Ranales
  Lauraceae
    Umbellularia salicifolia (Lesquereux) Axelrod
Rosales
  Hamamelidaceae
    Liquidambar pachyphyllum Knowlton
  Rosaceae
    Prunus treasheri new species
  Leguminosae
    Amorpha condoni Chaney
Sapindales
  Aceraceae
    Acer sp.
Rhamnales
  Rhamnaceae
    Rhamnus troutdalensis new species
Umbellales
  Cornaceae
    Cornus ovalis Lesquereux
Ebenales
  Ebenaceae
    Diospyros andersonae Knowlton
Gentianales
  Oleaceae
    Fraxinus caudata Dorf
Incertae sedis
    Phyllites plinerva new species

A total of 1046 specimens have been collected, of which 886 are from the Buck Creek locality, and 160 from Camp Collins. As is shown in table 30, the florules from the two localities have little in common; *Quercus winstanleyi* makes up three-fourths of the total at Buck Creek, but is only sparsely represented at Camp Collins; here nearly four-fifths of the specimens are referred to *Ulmus californica,* a species not recognized in the Buck Creek florule. These local differences might be less conspicuous if our collections were larger, but in the light of present knowledge they are interpreted to indicate a varied forest composition, as set forth below. It also seems probable that with larger collections the numerical representation of many species might be considerably altered.

In addition to the dominant *Quercus winstanleyi,* there are only 4 species in the Buck Creek florule which make up more than 1 per cent of its total. Fragmentary remains of a grasslike plant are numerous, and willows are locally more abundant in the record even than leaves of oak. Considering its rarity or absence in other Pliocene floras of the Northwest, the representation of *Sequoia langsdorfii* is surprisingly high. As will be suggested elsewhere, the trees from which these redwood twigs were derived probably lived in sheltered spots either along the main stream course, or more probably in side valleys. If the sediments at one of our collecting sites had been deposited opposite the

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mouth of such a tributary, there might have been more individual twigs in the record. The association of redwood specimens with those of riparian species like *Salix wildcatensis* and *Prunus treasheri* on our slabs, rather than with *Quercus winstanleyi,* supports the suggestion that *Sequoia langsdorfii* was a tree of ravines or stream margins rather than of the slopes.

As was stated above, the Camp Collins florule is made up largely of leaves of *Ulmus californica.* None of the other species are numerous in our collections.

TABLE 30

OCCURRENCE OF SPECIMENS AT TROUTDALE LOCALITIES

SPECIES	BUCK CREEK		CAMP COLLINS		TROUTDALE FLORA	
	No. of specimens	Per cent	No. of specimens	Per cent	No. of specimens	Per cent of total
Quercus winstanleyi	674	76.1	2	1.3	676	64.6
Ulmus californica	.....	.....	126	78.8	126	12.0
Cyperacites sp.	81	9.1	.....	.....	81	7.7
Salix wildcatensis	77	8.7	1	0.6	78	7.4
Sequoia langsdorfii	23	2.7	.....	.....	23	2.2
Prunus treasheri	16	1.8	.....	.....	16	1.5
Amorpha condoni	.....	.....	9	5.6	9	0.9
Pterocarya oregoniana	.....	.....	9	5.6	9	0.9
Diospyros andersonae	.....	.....	5	3.1	5	0.5
Fraxinus caudata	4	0.5	1	0.6	5	0.5
Zelkova oregoniana	.....	.....	4	2.5	4	0.4
Cornus ovalis	3	0.3	.....	.....	3	0.3
Rhamnus troutdalensis	.....	.....	3	1.9	3	0.3
Phyllites plinerva	2	0.2	.....	.....	2	0.2
Umbellularia salicifolia	2	0.2	.....	.....	2	0.2
Abies axelrodi	1	0.1	.....	.....	1	0.1
Acer sp.	1	0.1	.....	.....	1	0.1
Chamaecyparis gracilis	1	0.1	.....	.....	1	0.1
Liquidambar pachyphyllum	1	0.1	.....	.....	1	0.1
Total	886	100.0	160	100.0	1046	100.0

This florule represents a forest different in aspect from that at Buck Creek, but in view of the low total of specimens, we have no present basis for judging the relative abundance of most of its species.

There are inherent difficulties in considering the origin and physical significance of a flora represented by so few species and specimens. In contrast with the Miocene and older Tertiary floras of Oregon, this paucity of material characterizes most of the Pliocene floras as yet studied from the western United States. Such reduction in numbers of genera and species may well have resulted from the trend toward more extreme climate induced by topographic and other changes in later Tertiary time. A comparison of Miocene and Pliocene floras

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shows that large numbers of Middle Tertiary species disappeared in western North America at the close of the Miocene, and that many of those which survived were inconspicuous in Pliocene forests.

Although the division of the Troutdale flora into elements is less significant than in the case of floras with numerous species, this method of analysis presents the best means of establishing comparisons with living vegetation. *Acer* sp., *Cyperacites* sp., and *Phyllites plinerva* have been omitted from the list in table 31 because their modern relationships have not been established.

TABLE 31

ELEMENTS OF THE TROUTDALE FLORA

Fossil species	*Equivalent living species*
West American Element	
Amorpha condoni	A. californica Nuttall
Chamaecyparis gracilis	C. lawsoniana Parlatore
Cornus ovalis	C. californica C. A. Mey
Fraxinus caudata	F. oregona Nuttall
Salix wildcatensis	S. lasiolepis Bentham
Sequoia langsdorfii	S. sempervirens Endlicher
Umbellularia salicifolia	U. californica Nuttall
East American Element	
Amorpha condoni	A. fruticosa Linnaeus
Diospyros andersonae	D. virginiana Linnaeus
Liquidambar pachyphyllum	L. styraciflua Linnaeus
Quercus winstanleyi	Q. prinus Linnaeus
Ulmus californica	U. americana Linnaeus
East Asian Element	
Abies axelrodi	A. sutchuensis Rehder and Wilson
Cornus ovalis	C. walteri Wangerin
Diospyros andersonae	D. kaki Linnaeus
Prunus treasheri	P. davidiana (Carrière) Franchet
Pterocarya oregoniana	P. stenoptera DeCandolle
Quercus winstanleyi	Q. aliena Blume
Rhamnus troutdalensis	R. rugulosus Hemsley
Salix wildcatensis	S. phylicifolia Linnaeus
Zelkova oregoniana	Z. serrata Makino

It has not been practicable to subdivide the representatives of the West American Element into components, since several of them are wide-ranging and referable to more than one. A large representation of this element is to be expected in a Pliocene flora in northern Oregon. Farther south, Madro-Tertiary species are predominant in Pliocene floras, but with the possible exception of *Salix wildcatensis,* the Southwest American Element is not represented in the Troutdale flora. Typical coastal members of the West American Element are the two conifers, *Sequoia langsdorfii* and *Chamaecyparis gracilis.* Judging from their representation in our collections, neither of them was a common member of the forest. From a predominant position in the Bridge Creek flora, now considered to be of Upper Oligocene or Oligo-Miocene age, *S. langsdorfii* be-

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comes progressively less numerous in the Middle Miocene Latah and the Upper Miocene Mascall floras. Absent from the Lower Pliocene Dalles flora on the east side of the ancestral Cascade Range, and extremely rare in the Ellensburg flora from a more northerly position in the same geographic province, redwoods survived into late Tertiary time at this northern latitude largely on the coastal slopes of Oregon. It is possible that *Chamaecyparis gracilis* was somewhat more common than our record indicates, for the remains of this and related genera are seldom numerous in modern deposits even where trees are abundant on adjacent slopes; but in any event we have no basis for supposing that it was an important member of the Troutdale forest. The modern equivalent of *Umbellularia salicifolia, U. californica,* is limited eastward to the western slopes of the Sierra Nevada. Living species which correspond to our fossil ash, dogwood, and willow are widely distributed riparian species from British Columbia or northern California southward, on coastward slopes.

The climatic implications of the large representation of the East American and East Asian Elements are highly significant. Not only do these elements make up two-thirds of the species of the Troutdale flora, but included in them are its most abundant members, *Quercus winstanleyi* and *Ulmus californica.* Especially well represented is the East Asian Element, an element which is characteristic of such Miocene floras as the Latah and Trout Creek, and which current studies are showing to be abundant in the Mascall flora as well. No other post-Miocene flora in western North America is known to have an equal number of Asiatic equivalents. Modern equivalents of the fossil species making up these elements are now largely restricted to regions of summer rainfall, and all except the fir are deciduous. The presence of their Tertiary ancestors in the Pliocene deposits of northwestern Oregon seems to indicate that moderate climate of the Middle Tertiary type, involving rainfall well distributed throughout the year, continued in this region after it had been displaced by a more extreme seasonal regime in eastern Oregon and in California. Supporting this conclusion is the presence of *Sequoia langsdorfii* and *Chamaecyparis gracilis* in the Troutdale flora, species which ranged inland during Middle Tertiary time when precipitation was adequate at all seasons.

These conifers have been progressively restricted westward until their modern equivalents occur only along the coast,[1] where fogs provide compensation for a dry summer season. The Troutdale flora provides the latest record of association of the redwood and cedar with broad-leafed deciduous trees whose descendants are now largely confined to the summer-wet eastern sides of the northern continents. The relict occurrence of *Liquidambar pachyphyllum,* represented by a single leaf, is of particular interest because of its widespread representation in Miocene floras on the Columbia Plateau. Several leaves of this species have recently been collected in the Ellensburg formation near Selah, Washington, but it is unknown in floras younger than Lower Pliocene in the Tertiary of the Northwest. *Ulmus* lingered on in western North America until nearly the end

[1] There are limited occurrences of *Chamaecyparis lawsoniana* in the Siskiyou Mountains and on Mount Shasta.

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of the Pliocene; it has survived along streams in central Asia where summer rainfall is scant and irregular (Chaney, 1935*a*, p. 90, fig. 11), and it extends westward across the High Plains in North America into regions of low precipitation. For the most part, elms occur only in regions where precipitation is well distributed throughout the year. Several Troutdale genera such as *Cornus, Prunus,* and *Salix* regularly occur along stream courses in western North America, where they have a shrub habit. *Liquidambar, Ulmus, Diospyros, Pterocarya,* and *Zelkova* have, however, completely disappeared from the western United States, together with many other genera from the older floras of the John Day Basin which were eliminated at the close of the Miocene.

At the present time, the lower Willamette Valley has an equable climate. Annual precipitation averages 42.25 inches, of which the months of July and August receive 0.57 and 0.62 inches respectively.[2] During the 50 years for which records have been kept, rainfall has varied from only a trace to as much as 3.39 inches during one of these months. The average annual temperature is 53° F. There is some freezing weather every winter, but frost rarely occurs during the growing season. The vegetation in this region is dominated by conifers, broad-leafed evergreens, and thick-leafed deciduous trees. *Pseudotsuga taxifolia* (Lambert) Britton, *Tsuga heterophylla* Sargent, *Thuja plicata* D. Don, and *Pinus ponderosa* Douglas among the conifers, and *Alnus rubra* Bongard, *Acer macrophyllum* Pursh, *Quercus garryana* Douglas, *Q. kelloggii* Newberry, and *Arbutus menziesii* Pursh are the common members of the modern forest near the Troutdale fossil localities. These trees are widely distributed in the Pacific states in regions of limited summer precipitation. They are represented by equivalent fossil species in the Miocene floras of the Columbia Plateau. It seems clear that they have persisted in western North America because of their superior ability to withstand summer drought.

A question may be raised as to why certain of the Troutdale species have not survived along the narrow coastal strip west of the Coast Range, about 50 miles west of the fossil localities. The annual rainfall there[3] is nearly twice that near the fossil locality, with over 6 inches falling during the summer months as compared with less than 3 inches at Portland. The annual average temperature is about 2° lower, and there is little freezing or snow. In such an environment we might expect to find the Pliocene oak, elm, sweet gum, and persimmon still represented by their modern equivalents. A possible cause for their disappearance may have been the more extreme climate of intervening Pleistocene time (see LaMotte, 1936, pp. 94–95). Another unfavorable aspect of modern climate may be the lack of low winter temperatures along the Oregon coast. Many broad-leafed deciduous trees of the eastern states appear to be benefited by periods of subfreezing temperature in their normal ranges; even in California, where they grow as exotics, better growth has been noted after an exceptionally cold winter. The problem of the disappearance of Tertiary species from certain

[2] Data for Portland, in *Climatic summary of the United States.*

[3] Based on records for Astoria, Fort Stevens, Nehalem, Tillamook, and Tillamook Rock.

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apparently favorable situations in western North America is clearly one for which no satisfactory solution may now be presented.

The Pliocene climate of the lower Willamette Valley, as indicated by the Troutdale flora, is in marked contrast with that of the preceding epoch. The flora of the Molalla formation is now being studied by Wilder, who assigns it to a Lower Miocene horizon on the basis both of fossil plants and of invertebrates. This flora includes most of the Troutdale genera, but the species are relatively large-leafed and are interpreted as indicating higher temperature and precipitation. Other genera not recorded in the Troutdale flora support the suggestion of more favorable conditions for forest growth during the Molalla stage. This is consistent with the known trend in climate in western North America, as discussed elsewhere. The Troutdale flora occupies an intermediate position between the warm, moist floras of the Miocene and the vegetation of today in the Willamette Valley, where summer rainfall is greatly reduced.

The marked difference in composition between the two Troutdale florules reflects the varied topography which was developing along the axis of the Cascade Range during later Tertiary time. Prevalence of volcanism is indicated by widespread flows and pyroclastic accumulations, of which the Troutdale and Dalles formations are a part. The locally coarse texture of these formations indicates high relief such as might be expected on the flanks of active volcanoes. Judging from the composition of the Buck Creek florule, the part of the Troutdale formation in which it occurs was laid down on the flood plain of a valley where white oaks were predominant, together with riparian species such as willow and cherry. In the outer Coast Ranges of California, relict patches of redwoods and their associates are of regular occurrence along small tributary streams which flow down the steep valley slopes to the flood plains below. The occurrence in the Buck Creek florule of a minority element of *Sequoia langsdorfii, Chamaecyparis gracilis,* and *Umbellularia salicifolia* is strongly suggestive of topography like that shown on plate 56, figure 1, where redwoods and California laurel extend down from the side canyons to mingle with oaks on the lower slopes and with flood-plain trees below. Northward in the inner Coast Ranges, valley oaks are locally the most abundant trees along the flood plains. As elsewhere stated, these oaks (*Quercus lobata*) are less similar to the Troutdale oak than is *Q. aliena* of China. This occurrence, however, as shown on plate 56, figure 2, suggests the general setting of the Buck Creek site of fossil accumulation, with redwoods on distant slopes above, where their leaves may occasionally enter the sedimentary record.

No modern occurrence of elms comparable with the Camp Collins florule can be cited in western North America, where *Ulmus* no longer occurs as a native tree. Several species of elm, however, are typical members of the slope forest in the eastern United States and in eastern Asia. In Hupeh and Szechwan, China, *Pterocarya stenoptera* is described by Sargent as "one of the commonest trees on river-banks and on the stony and sandy beds of summer torrents" (1917, p. 181); its Pliocene equivalent would therefore have been a

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compatible associate of *Ulmus californica* and the other members of the Camp Collins florule, the whole assemblage suggesting a slope habitat more exposed than that occupied by the oaks of the Buck Creek florule.

The evidence regarding the Troutdale environment may be summarized as follows:

1. The climate was characterized by summer rainfall, certainly less than during the Miocene, but more than during post-Lower Pliocene time on the Columbia Plateau. An annual precipitation of 35 inches is indicated. Judging from such members as redwood, persimmon, sweet gum, and liu-shu (*Pterocarya*), the temperature was not unlike that on the adjacent coast of Oregon at the present time, where there is a low seasonal range, and a mean annual temperature slightly higher than 50° F.

2. The topography was of the diversified type found on the flanks of a range of volcanoes. Valleys with well developed flood plains and rather high gradients had steep adjacent slopes and tributary ravines. These valleys extended westward across a coastal plain, unbroken by intervening ridges such as the Coast Ranges of today.

Age of the Flora

The determination of the age of the Troutdale formation is made difficult by the scarcity of other near-by Pliocene floras for comparison. The lack of fossil mammals in the Troutdale is a further handicap. There is, however, so close a resemblance between the Troutdale flora and the floras from the Ellensburg and Dalles formations that its Lower Pliocene age may be considered to be well established.

Reference to table 32 indicates that 5 of the Troutdale species are found in the Ellensburg flora, and 4 in the Dalles. These two floras from the east slopes of the ancestral Cascade Range have 6 species in common, including several of their most characteristic members. In addition, their close age relationship is indicated by mammalian fossils, with *Hipparion condoni* in common, and several other forms which indicate a Lower Pliocene age. The Troutdale flora contains only 2 species which occur in both the Ellensburg and the Dalles formations, but these are the highly characteristic *Quercus winstanleyi* and *Ulmus californica*. The total number of Troutdale species represented in the combined floras from east of the Cascades is 7, or half of its total having outside distribution.

The survival of several Miocene species into the Troutdale stage, including members of the East American and East Asian Elements, has already been noted. Of the former, there may be mentioned *Liquidambar pachyphyllum* and *Diospyros andersonae*, with *Quercus mccanni* and *Ulmus speciosa* also showing close relationship to the Troutdale species *Q. winstanleyi* and *U. californica*. *Zelkova oregoniana* is the only member of the East Asian Element with Miocene occurrence, but *Quercus mccanni* also shows Asiatic affinities. The greatest number of Troutdale species with Miocene occurrence fall into the West American Element; these include *Chamaecyparis gracilis, Cornus*

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TABLE 32

OCCURRENCE OF TROUTDALE SPECIES IN OTHER TERTIARY FLORAS

SPECIES	OLIGO-MIOCENE	MIOCENE			TRANSITIONAL				PLIOCENE									
		LOWER	MIDDLE	UPPER					LOWER						MIDDLE		UPPER	
	Bridge Creek	Eagle Creek	Latah	Mascall	Lower Idaho	Neroly	Remington Hill	Table Mountain	Dalles	Ellensburg	Alvord Creek	Verdi	Ogallala	Black Hawk Ranch	Oakdale	Mulholland	Wildcat	Sonoma
Amorpha condoni	..	..	..	..	..	..	..	..	x	..	x	..	..	..	..	..	..	x
Chamaecyparis gracilis	..	..	..	x	..	..	x	..	..	..	..	..	..	..	..	..	..	..
Cornus ovalis	x	..	x	..	..	..	..	x	..	..	..	..	..	..	..	x	..	..
Diospyros andersonae	..	..	x	x	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Fraxinus caudata	o	..	o	o	o	..	..	..	..	x	..	o	o	..	..	x	x	x
Liquidambar pachyphyllum	o	x	x	x	..	..	x	..	..	x	..	..	..	..	..	..	..	..
Prunus treasheri	..	..	..	..	..	x	..	..	..	..	..	..	..	..	..	..	..	..
Pterocarya oregoniana	o	..	o	o	..	..	..	..	x	..	..	..	..	..	..	..	..	..
Quercus winstanleyi	..	..	o	o	o	..	x	..	x	x	..	..	..	..	..	..	..	..
Salix wildcatensis	..	..	..	..	..	..	..	..	..	..	..	..	o	..	x	x	x	x
Sequoia langsdorfii	x	..	x	x	x	..	x	..	..	x	..	..	..	..	..	..	x	x
Ulmus californica	o	o	o	o	x	..	x	x	x	x	..	..	o	x	..	..	..	..
Umbellularia salicifolia	..	..	x	x	..	x	x	x	..	..	..	..	..	..	x	x	x	x
Zelkova oregoniana	o	..	x	x	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Total in flora	2	1	6	6	2	2	6	3	4	5	1	0	0	1	2	4	4	5
Total in stage	2	1	6	6	8				7						4		5	
Total in epoch	2	7			8				10									

x = identical species; o = related species.

ovalis, Sequoia langsdorfii, and *Umbellularia salicifolia.* A total of 6 Troutdale species are recorded from the Middle Miocene Latah formation, and 5 from the Upper Miocene Mascall; only 1 Troutdale species is known to occur in the Lower Miocene Eagle Creek formation. Of the Troutdale species with Miocene occurrence, only *Zelkova oregoniana* and *Diospyros andersonae* have been previously limited to that epoch.

The Miocene affinities of the Troutdale flora are further emphasized by its resemblance to several floras transitional in age between the Miocene and Pliocene, with a total of 8 species in common. The closest relationship is shown by the Remington Hill flora from the west slope of the central Sierra Nevada; the higher altitude of this California flora compensated for its lower latitude, giving it a climate similar to that at lower levels on coastal slopes farther north.

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The Table Mountain and Neroly floras of central California, from successively lower altitudes, show less resemblance to the Troutdale; and the Lower Idaho flora of Idaho also has little in common.

A total of 11 species, about four-fifths of those with outside distribution, have been recorded from Pliocene floras. These include *Amorpha condoni, Fraxinus caudata, Pterocarya oregoniana,* and *Salix wildcatensis,* which are not known from horizons older than the Pliocene, together with *Prunus treasheri,* which also ranges down into deposits of transitional age. A majority of the Troutdale species known to occur elsewhere in the Pliocene are assignable to the West American Element; these include *Amorpha condoni, Cornus ovalis, Fraxinus caudata, Salix wildcatensis, Sequoia langsdorfii,* and *Umbellularia salicifolia.*

Only a slight resemblance is apparent between the Troutdale and such geographically remote Lower Pliocene floras as the Black Hawk Ranch and Ogallala. It should be noted, however, that both of these floras include elm, one of the more abundant species of the Troutdale flora. There is little in common with the Alvord Creek flora of southeastern Oregon, which comes from a geographic province that was almost as different during the Pliocene as it is today. The closest affinities are with the near-by Ellensburg and Dalles floras, both of which lived on the eastern slope of the ancestral Cascades, but nonetheless in environments somewhat conditioned by the Pacific. This is more the case with the Ellensburg than with the Dalles flora; redwood and sweet gum both survived into the Lower Pliocene of eastern Washington, a fact which suggests that there was a broad valley extending landward into this region, carrying certain elements of coastal climate inland. The dominant species of the Troutdale flora are with few exceptions known to occur in one or both of these floras from the eastern slopes of the Pliocene Cascades in Oregon and Washington.

A rather marked relationship is apparent to the Mulholland flora of west-central California. This Middle Pliocene flora has been shown to have been affected to some extent by its proximity to the ocean, with resultant summer precipitation (chap. 5, pp. 115–116). The 4 species in common between the Troutdale and Mulholland floras are all related to modern species which have survived in riparian habitats in western North America, a fact which suggests that the relationship between these floras is primarily dependent on their similarities of local environment and has no close age significance. The total of 5 species in common with the Upper Pliocene Sonoma flora is likewise an expression of similar coastal environments; the modern equivalents of the Troutdale species involved are all living today near the coast in central California. The redwood has been restricted more than 200 miles south since the Troutdale stage, and the modern California laurel is also more southerly in distribution.

The strongest evidence of the age of the Troutdale flora is its close relationship to the adjacent Dalles and Ellensburg. Differences between these floras from opposite sides of the ancestral Cascades are explainable in terms of topographic rather than age discrepancies. For the Troutdale flora lived in a region where ocean control of climate persisted longer than on the landward slopes of the mountains, and must have retained survivors from the Miocene

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longer than the Dalles and Ellensburg farther inland. The somewhat larger size of the leaves of *Amorpha condoni* and *Ulmus californica* in the Troutdale as compared with the Dalles is also consistent with their differing geographic positions. Close relationships to California floras of earlier age reflect the progressive shifting of this coastal climate southward in later Pliocene time, as recorded by the Mulholland and Sonoma floras. The stratigraphic position and structure of the Troutdale formation are consistent with its correlation with the Dalles and Ellensburg formations. Though exact contemporaneity can perhaps not be finally established until additional paleontological evidence becomes available, the relations of the three floras on the flanks of the Cascades are sufficiently close to indicate that all of them lived during the time immediately following the close of the Miocene, when profound physical changes were leaving their mark on the vegetation of the Columbia Plateau.

Several previous references to the Troutdale formation have assigned it a Pleistocene age. Williams (1916, pp. 119–121, 128–129) and Bretz (1917, pp. 452–454, 457–458) have referred it to the Pleistocene, partly by correlation with the Satsop formation as known from the Chehalis valley of western Washington, and also on the basis of its fossil plants. These authors extended the "Satsop" eastward to include gravels near The Dalles, and have suggested that the Dalles formation may represent a local phase. Subsequent studies by Buwalda and Moore (1927, p. 236; 1930, pp. 18–21) have indicated that the gravels of the Cascade Range along the Columbia Gorge are not to be correlated with the Satsop of Washington, and are of much greater age. The paleobotanical evidence presented by Williams and Bretz was based on collections made by the writer, and is summarized by Bretz as follows (1917, pp. 457–458):

> A clay stratum with abundant fossil leaves has been found in the Satsop formation on the western slope of the Cascade Range. Knowlton has examined collections from this bed and is of the opinion that the flora is Quaternary in age. He finds leaves of *Quercus venustula* and *Sequoia sempervirens* in the collection. Both are living species.

Resemblances of the Troutdale oak and redwood to *Q. venustula* Green (=*utahensis* Rydberg) and *S. sempervirens* Endlicher are no closer than to Tertiary species of oak and redwood. If close similarity to living species were a sound criterion for Pleistocene age, many Tertiary deposits dating as far back as the Eocene would also be referable to the Quaternary. Actually the Troutdale oak is much more nearly related to half a dozen other living species of eastern North America and eastern Asia than to *Q. venustula;* the ancestors of these modern oaks, with closely similar leaves, are recorded as far back as early Miocene time. The presence of *Sequoia* at the latitude of Portland during the Pleistocene is completely at variance with all that is known regarding later Cenozoic climates in the western United States. Other members of the Troutdale flora, discovered since the studies of Bretz and Williams, are likewise out of accord with the known facts of Pleistocene climate and plant distribution, and indicate an age not younger than Lower Pliocene. The age interpretation of

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these authors may therefore be set aside on both inorganic and organic evidence.

More recently Hodge has referred the Troutdale formation to "probably earliest Pleistocene" (1938, pp. 873–877). He restricts it to the "great piedmont fan deposit lying on the west side of the Cascade zone," but states that in many places it is indistinguishable from the Dalles formation, and was deposited contemporaneously. It may therefore be concluded that he considers the Troutdale as of essentially the same age as, or slightly younger than, the gravels and pyroclastic deposits described by others along the Columbia Gorge east to The Dalles. His basis for this age reference is the occurrence of the Troutdale formation "in very youthful valleys in the Coriba Surface," its structural anomalies with the Columbia River basalt, and the character of the fossil flora as reported by Williams in 1916; he correlates it with the Shutler formation, whose mammalian fauna and stratigraphic position seem to establish its Pleistocene age. Our findings, based on comparison with the Dalles and Ellensburg floras, and on our interpretation of the structure of all these formations, place the age of the Troutdale as Lower Pliocene.

This reference is in accord with the opinion of Buwalda and Moore (1927, p. 236), who have correlated the gravels of the Cascade Range along the Columbia Gorge with the Dalles and Ellensburg formations, and have suggested a new name, Hood River conglomerate, for them. They point out that the Hood River gravels are overlain by both the Dalles and the Ellensburg, and that they represent the older part of these formations. The mammalian fauna of the Ellensburg formation has been interpreted as indicating an Upper Miocene to Lower Pliocene age (Buwalda and Moore, 1930, p. 17). Judging from paleobotanical evidence as yet unpublished, and summarized in table 33, the writer believes that the Ellensburg formation is of Lower Pliocene age, although its transitional Mio-Pliocene age may be established by future studies.

Warren (1941) has recently studied the Hood River conglomerate of eastern Washington, and has reached the conclusion that it is the equivalent of the Dalles and Ellensburg formations, representing the sediments of the master stream whose tributaries were depositing these piedmont fans. He has presented additional data regarding its lithology, structure, and distribution, and has shown that it lies beneath the uppermost flow of the Yakima (Columbia River) basalt at several localities. Mammalian fossils found in the Hood River conglomerate indicate a late Miocene or early Pliocene age. Warren does not refer to the Troutdale formation, but his correlation of the Hood River conglomerate with the Satsop of Bretz and Williams indicates that he is referring to beds partly or wholly equivalent.

Treasher's recent paper on the geologic history of the Portland area (1942) contains an excellent description of the Troutdale formation and a map showing its distribution. He has mistakenly quoted the writer as believing that the flora of the Troutdale indicates a Middle Pliocene age. All the evidence which he presents seems consistent with the reference of the Troutdale formation to the Lower Pliocene, although his opinion may be correct, as expressed in a

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recent letter, that the "Troutdale should perhaps represent the later stages of the Dalles and Hood River, and may have been deposited in part after deposition of the eastern formations ceased."

The scarcity of floras younger than Miocene in the Pacific Northwest makes any close assignment of age tentative, and subject to possible revision when collections have been made from many localities. If there were available for comparison several Middle Pliocene floras from this region, relationships might be apparent which would lessen the age of the Troutdale as here assigned; it is even possible that if we had more floras transitional in age between the Miocene and Pliocene, we might refer the Troutdale to a slightly older horizon. At present we can only say that its close resemblance to the Dalles and Ellensburg floras, the type of climate indicated by its constituents, and the lithology, stratigraphic occurrence, and structure of the beds in which it occurs, all point toward the Lower Pliocene age of the Troutdale flora.

Summary

The Troutdale formation, accumulated as alluvial fans and channel deposits on the western borders of the rising Cascade Range, is essentially equivalent in age to the Dalles formation of the interior. Unlike the Dalles flora, the Troutdale includes a strong representation of trees whose modern equivalents live in regions of summer rainfall; these are assigned to the East American and East Asian Elements. Several abundant species represent modified descendants of large-leafed Miocene forms. *Sequoia langsdorfii* and other conifers are sparsely represented. This assemblage, intermediate in aspect between the humid Miocene and the summer-dry vegetation of today, indicates local survival of the relatively favorable climate of earlier Tertiary time as late as Lower Pliocene time in western Oregon.

SYSTEMATIC DESCRIPTIONS

Phylum SPERMATOPHYTA
Class GYMNOSPERMAE
Family PINACEAE

Abies axelrodi new species

(Plate 57, figure 5)

Description. Twig slender, 4.5 cm. long, incomplete at both ends, probably terminal. Leaves 8 to 11 mm. long, the largest nearly 2 mm. broad, acute at their bases and with blunt tips; closely spaced along the upper two-thirds of the twig, with the basal 1.5 cm. bare; attached spirally on the twig by a short, somewhat enlarged petiole; medial groove well developed; texture thick.

Discussion. This specimen differs from other conifers in the Troutdale collections in having relatively short, bluntly pointed needles, closely spaced on the twig. Even more critical evidence for separating them from *Sequoia langsdorfii* is their spiral attachment on short petioles. These characters are indicative of *Abies,* a genus rep-

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resented by several species in the Tertiary of western North America. If additional specimens were available, it could be more positively determined whether the dimensions of the needles are typical; if that is the case, *A. axelrodi* is wholly unlike any previously described species of fossil fir, and without any closely similar living equivalent in North America. Several species now growing in Asia have equally short and broad leaves; the most similar to the Troutdale specimen is *A. sutchuensis* Rehder and Wilson, an alpine species from western Kansu, China.

Leafy twigs referred to *Sequoia obovata* Knowlton, from the Cretaceous Vermejo formation of Colorado and New Mexico and from the Cretaceous of Alaska, are suggestive of the present species, but the leaves appear to be decurrent, as should be the case if they are correctly referred to *Sequoia;* they are also less closely spaced on the twigs than those of *A. axelrodi.*

This species is named in honor of Dr. D. I. Axelrod, who first suggested that it was referable to the genus *Abies.*

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2584.

Family TAXODIACEAE

Sequoia langsdorfii (Brongniart) Heer

(Plate 57, figure 2)

Sequoia langsdorfii (Brongniart) Heer, Flora tertiaria Helvetiae, vol. 1, p. 54, pl. 20, fig. 2; pl. 21, fig. 4, 1855.

Twigs of this widely distributed Tertiary species are numerous, and more than half of them show evidence of wear before burial. As has been suggested elsewhere, redwoods seem not to have been abundant near the Troutdale sites of deposition, but were probably restricted to sheltered side canyons and protected slopes. This habitat characterizes modern redwoods on the eastern border of their range (see pl. 56, fig. 1).

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2585.

Family CUPRESSACEAE

Chamaecyparis gracilis Condit

(Plate 57, figure 3)

Chamaecyparis gracilis Condit, Carnegie Inst. Wash. Pub. 553, pp. 39–40, pl. 4, fig. 2, 1944 (see synonymy).

A terminal twig with several branchlets is definitely referable to *Chamaecyparis* on the basis of the shape and arrangement of the leaves. The lateral leaves are more slender than the medials, and meet along the central axis of the stem, thus separating the rounded medial leaves.

This specimen shows the keeled medial leaves, and their short appressed tips. It is somewhat coarser than the specimen figured by Condit, and with the lateral leaves more spreading. But with the material available there is no basis for considering that it represents a new species.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2586.

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Class ANGIOSPERMAE
Subclass MONOCOTYLEDONES
Family CYPERACEAE

Cyperacites sp.

(Plate 57, figures 1, 4)

Numerous fragments of this large grasslike plant give little clue as to its characteristics or biologic relationships. All the specimens are prominently ribbed. Their relative abundance in the Troutdale flora is suggestive of open conditions on a flood plain where most of the trees were confined to the stream borders. This is in contrast with the more heavily forested valleys of the Miocene and older Tertiary, when grasses made up a negligible part of the vegetation as judged from their scarcity in the fossil record.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2587, 2588.

Subclass DICOTYLEDONES
Family SALICACEAE

Salix wildcatensis Axelrod

(Plate 58, figure 2; plate 59, figures 1–4)

Salix wildcatensis Axelrod, Carnegie Inst. Wash. Pub. 553, p. 132, 1944 (see synonymy and discussion).

Collections at the Buck Creek locality include numerous entire-margined leaves which appear to be referable to this species from the Pliocene of California. The leaves vary considerably in shape and size, but all fall within the normal limits of variation of a common entire-margined living species, *Salix lasiolepis* Bentham, which ranges from northern California into Arizona and Mexico (see University of California Herbarium sheets 469423, 482237). Two other modern California species, *S. breweri* Bebb and *S. coulteri* Andersson, have entire-margined leaves resembling the fossil specimens. A Chinese species, *S. phylicifolia* Linnaeus, also appears to be related.

Relationship is apparent to one of the specimens of *Salix miosinica* Hu and Chaney from the Shanwang flora of Shantung, China (1938, pl. 4, fig. 4).

Occurrence. Buck Creek, loc. 5; Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2589, 2590, 2591, 2592, 1695 (loc. 5).

Family JUGLANDACEAE

Pterocarya oregoniana new species

(Plate 57, figure 6; plate 58, figures 1, 4)

Description. Leaflets oblong lanceolate; 8.0 to 10.0 cm. long, 3.0 to 3.5 cm. wide, with greatest width at about the middle of the leaflet; apex acute or bluntly rounded; base asymmetrical, acute on one side, rounded on the other; petiolules extremely short, with leaflets essentially sessile; midrib slender; numerous alternate secondaries departing at high angles at the base, 45° to 50° farther up, curving upward and

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forming loops well within the margin with the secondary above; percurrent tertiaries enclosing fine polygonal mesh, at the margin extending from the looping secondaries to the teeth; margin with many small crenate-serrate teeth; texture firm.

Discussion. Living members of this genus are restricted to central and southern China, extending westward to Szechwan and Yunnan. The fossil leaflets closely resemble those of *Pterocarya stenoptera* DeCandolle, which Sargent describes as one of the most common trees in valleys of central China.

There is some question whether *P. oregoniana* is distinct from *P. mixta* (Knowlton) Brown, described from the Latah formation and placed in new combination by Brown (1937*a*, p. 170, pl. 47, figs. 2, 3). The leaflets which he figures are much smaller than the Troutdale ones, and are less slender; when more complete material is available for study, these two species from the Tertiary of western North America may prove to be identical.

A rather marked resemblance may be noted between the Troutdale leaflets and those figured as *Juglans nigella* Heer from the Kenai formation of Alaska (Heer, 1869, p. 38, pl. 9, figs. 2–4; Hollick, 1936, pp. 81–82, pl. 38, figs. 1–5). Comparative studies with the specimens themselves will be necessary before their relationships can be accurately judged.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, nos. 2593, 2593*a* (counterpart); paratypes, nos. 2594, 2594*a* (counterpart), 2595.

Family FAGACEAE

Quercus winstanleyi new species

(Plate 60, figures 1, 3–5; plate 61, figures 1, 2, 4; plate 62, figure 2)

Description. Leaves obovate to oblanceolate; length 2.1 to 11.0 cm., width 0.9 to 5.2 cm.; tip narrowly to bluntly rounded; base acute to rounded; petiole medium to strong, up to 1.3 cm. long; from 5 to 11 pairs of alternate, rarely subopposite, secondaries leaving the midrib at angles of from 30° to 50°, rather closely and evenly spaced, straight; lobes simple, essentially symmetrical, varying from shallow on large leaves to deeper on small ones, from one-seventh to one-third of the width of the blade; lobes deepest at the widest part of the blade, becoming shallow or mere undulations toward the apex; lobes mostly rounded, pointing toward the apex, on some leaves tapering to a bluntly acute tip, somewhat reflexed; tertiaries percurrent; nervilles forming an irregular mesh; texture medium to thick.

Discussion. There are times in the life of every paleontologist when difficulties involved in the sound treatment of his material become insurmountable. At such times it is necessary to make decisions which are not wholly consistent with all the known facts, and which may be at variance with the best taxonomic procedure. Such a compromise seems inescapable in the case of the oak leaves of the Troutdale flora, which we are describing as a new species in spite of close resemblances to previously described Tertiary oaks.

This species is the most abundant in our collections from the Buck Creek locality, so we are not handicapped by lack of material. The problems regarding the Troutdale oak which have been troubling us for several years, problems not fully solved in this paper, arise from the inadequate record of related species of fossil oaks, and from the difficulty in drawing species distinctions on the basis of leaves among similar species of oaks now living. This general problem has been discussed in

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chapter 1 of this report, and will be considered here in somewhat greater detail.

The white oak leaves in the Troutdale flora are characterized by wide variation in size. The leaf shown as figure 2 on plate 62 is fully as large as those referred by Berry to *Quercus mccanni,* from the Latah formation at Grand Coulee, Washington (1931, p. 36, pl. 11, figs. 5–7); its shape, nervation, and margin are so similar to those of the specimens of *Q. mccanni* shown as figures 5 and 7 that there is no sound basis for distinguishing them. Our first alternative is to assign this large Troutdale leaf and others of similar size to *Q. mccanni.* Another white oak, *Q. columbiana* Chaney, from the Eagle Creek formation of northern Oregon (1920, p. 170) and reported also from the Latah formation (Brown, 1937*b,* pp. 508–509), is of a similar type and is difficult to distinguish either from *Q. mccanni* or from our large specimens. We have considered the desirability of placing Berry's species in synonymy, and of referring our Troutdale material also to *Q. columbiana;* the specimen represented by figure 2 in the Eagle Creek paper is not readily separable, but additional material collected by Wilder at a Lower Miocene locality in northwestern Oregon indicates that *Q. columbiana* as now known may have a broader shape and more rounded lobes than does the type specimen.

Resemblance of our specimens of *Q. winstanleyi* to leaves of modern white oaks and chestnut oaks is a further reason for considering the Troutdale species to be closely related to *Q. mccanni* and *Q. columbiana.* For all three species have the leaf form characterizing *Q. prinus* Linnaeus of the eastern United States, and *Q. aliena* Blume and *Q. fabri* Hance of eastern Asia, as well as other species of both regions. Berry has pointed out similarities between *Q. mccanni* and three Mexican species, *Q. chartacea* Trelease, *Q. martensiana* Trelease, and *Q. prinopsis* Trelease. None of these species seem to the writer as closely related to the three fossil species as are *Q. prinus, Q. aliena,* and *Q. fabri;* two of the Mexican species are larger, all appear to be more coriaceous (*chartacea* is partly evergreen), and there are minor differences in shape and margin. There seems to be sound evidence for considering our three fossil species to be on the ancestral line of modern species of white or chestnut oak now living in temperate North America and Asia. Our difficulty in the treatment of Tertiary specimens, as stated in the introductory chapter, is to determine whether there are natural boundaries along this line of descent.

When we come to consider the great majority of the white oak leaves in the Troutdale flora, marked differences in size are apparent which serve to distinguish them from the two Tertiary species mentioned above. The average length of 166 specimens in the Troutdale flora, representing all the leaves sufficiently well preserved to indicate their true size, is 5.5 cm. All these leaves form a continuous series, from the smallest, with a length of 2.1 cm., to the largest, which is 11 cm. long; 123 leaves, comprising 74 per cent of the total, fall within the size limits 4.0 and 7.0 cm.; 13 leaves, or 8 per cent of the total, are less than 4.0 cm. in length; 30 leaves, or 18 per cent of the total, are more than 7.0 cm. long; there is no basis other than size for separating the large leaves from those of intermediate or small size, for all have similar shape, nervation, and margin. The possibility has been considered that the smaller leaves are immature, and that they may have entered the record during the spring when one or more trees were uprooted, resulting in the burial of their partly developed leaves in alluvial deposits. Supporting this suggestion is the fact that the occurrence of the small leaves in the Troutdale sediments is patchy, and that the smallest and largest leaves do not commonly occur together on the same slabs. A further indication of their immaturity is the relatively heavy secondary nervation of

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the small leaves, and their rather slender, elongate lobes; partly developed leaves of living chestnut oaks have a similar appearance. If we could be sure that the small leaves were actually immature, and if we could assume that when mature they would closely resemble the larger Troutdale leaves, there would be little question regarding the propriety of assigning all these oak leaves to *Q. mccanni* or *Q. columbiana.* But there are no leaves of other Troutdale species which seem to be immature. The predominance of small leaves, and their intergradation with those of medium and large size, suggests that we are dealing with a small-leafed oak.

Differences in shape and margin are not sufficiently constant to separate *Q. winstanleyi* from the Miocene oaks, for they fall well within the limits of variation of such related living species as *Q. prinus* and *Q. aliena.* But on the basis of average size, *Q. columbiana* may be readily distinguished from *Q. winstanleyi:* the average length of the 21 specimens available for measurement in the Molalla flora is given by Wilder as 8.0 cm.; the smallest leaf is 4.5 cm. long, and the largest 14.0 cm.; with no leaves under 4.0 cm. in length, there are 8 specimens, or 38 per cent of the total, which fall within the size limits 4.0 and 7.0 cm., and 13 specimens, or 62 per cent of the total, which are more than 7.0 cm. long. There are only 5 specimens of *Q. mccanni* available for measurement; these average 7.5 cm. long, with 2 leaves under 7.0 cm. and 3 over 7.0 cm. long. Clearly, both the Miocene species are larger than *Q. winstanleyi,* and the percentages of their leaves which are of large size are much higher.

This difference in size between Miocene and Pliocene leaves has been noted in several other genera, for example *Celtis, Populus, Prunus,* and *Ulmus.* Reduction in size of Pliocene leaves is consistent with other evidence which indicates a trend toward lower rainfall in the western United States during later Tertiary time. By assigning our Pliocene material to a separate species, we emphasize this climatic change and provide a quantitative basis for distinguishing it from white oak leaves of Miocene age. The disadvantage of this procedure is that it serves to emphasize a difference between Miocene and Pliocene oaks which is at best slight, and which larger future collections may show to be nonexistent. It might be said by a critic concerned with establishing an age other than Pliocene for the Troutdale flora that our designation of a new species establishes a circuitous course of argument, in which inconsiderable or imaginary differences are relied upon to demonstrate a preconceived age concept. We are running the risk of such an error in our treatment of *Q. winstanleyi,* but this alternative seems better to fit all the evidence than naming two species of white oak in the Troutdale flora, or than assigning all the Troutdale specimens to Miocene species.

A significant argument in favor of naming *Q. winstanleyi* as a distinct species is added by consideration of the relationships of the blue oak, *Q. douglasii* Hooker and Arnott, of California. The leaves of this species are highly variable (Jepson, 1910, p. 215), including some with simple, rounded lobes highly suggestive of *Q. winstanleyi,* though these are fewer than is normal for the fossil species. Immature leaves on a specimen from Mount Shasta (University of California Herbarium sheet 61645) are highly suggestive of the smaller leaves of *Q. winstanleyi.* The blue oak now lives on dry, rocky slopes of the Sierra Nevada and inner Coast Ranges, in a habitat much less mesic than that occupied by *Q. prinus* of the eastern United States, or by *Q. aliena* of eastern Asia, which closely resemble the Miocene oaks. Its leaves may be as long as 7.5 cm., but the average size is about 4.5 cm. A small leaf of *Q. winstanleyi* from the Dalles flora, and another from the Ellensburg flora of Wash-

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ington, resemble certain leaves of *Q. douglasii* in having fewer and blunter lobes than most of our fossil specimens.

Summarizing the Tertiary record of simple-lobed white oaks, we suggest the following phylogenetic lines: The oldest oaks of this type are recorded from the Eocene of Alaska. Specimens of *Q. furuhjelmi* figured by Heer (1869, p. 32, pl. 5, fig. 10; pl. 6, figs. 1, 2), especially his figure 2 on plate 6, are larger than any of our specimens, but the resemblance is otherwise close. Hollick's figure of this species (1936, p. 98, pl. 55) is still larger, but appears to represent another species, and probably another genus. Leaves figured by Heer (1869, p. 32, pl. 6, figs. 3–5) and by Hollick (1936, p. 98, pl. 54, figs. 4, 5) as *Q. pseudo-castanea* Goeppert resemble in size and general aspect certain of the Miocene leaves from the western United States. These younger species, with *Q. columbiana* ranging through the Miocene in Oregon, Washington, and Idaho, and *Q. mccanni* from Middle to Upper Miocene, are replaced by *Q. winstanleyi* in the Mio-Pliocene of California and Lower Pliocene of Oregon, and by the still smaller-leafed *Q. douglasii* in the living flora of California. Characterized by a reduction in leaf size, and in the living species by a reduction in number of lobes, the modifications in foliage of these western oaks may be interpreted as a response to a changing environment, from the humid, summer-wet climate of the Miocene to the semiarid, summer-dry climate of the Arid Transition zone of California.

On the eastern side of the continent, where a climate with summer rainfall has persisted, oaks with leaves like those of the Miocene have continued to grow, including such species as *Q. bicolor* Willdenow, *Q. muhlenbergii* Engelmann, and *Q. prinus*. In eastern Asia there are also surviving several species of simple-lobed white oaks, of which *Q. aliena, Q. fabri,* and *Q. mongolica* Fischer are especially close to our Tertiary fossil species. In Europe a related living species is *Q. sessiliflora* Salisbury. These modern species of Eurasia may have descended from *Q. pseudo-castanea* Goeppert, whose oldest record is in the Eocene of Alaska. It has been recorded from the Miocene of Germany, France, Italy, Greece, and southern Russia. I am indebted to Roland W. Brown for information regarding the appearance and distribution of this species, and of the similar *Q. senogalliensis* Massalongo.

Occurrence. Buck Creek, loc. 5; Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Palebot. Ser., cotypes, nos. 1690, 1691, 1692, 1693, 2596, 2597, 2598, 2599; no. 1694 (loc. 5).

Family ULMACEAE

Ulmus californica Lesquereux

(Plate 63, figure 4)

Ulmus californica Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, pp. 15–16, pl. 4, figs. 1, 2; pl. 6, fig. 7*a*, 1878.

Condit, Carnegie Inst. Wash. Pub. 553, p. 46, pl. 8, fig. 4, 1944 (see synonymy).

The problem of the elm leaves of the Troutdale flora has been discussed in chapter 1 of this volume, and reasons have been set forth for assigning them to *Ulmus californica.* The distinctions between it and two other related species of fossil elm, the older *U. speciosa* Newberry and the younger *U. moragensis* Axelrod, are largely in size, but there is also a tendency toward broader leaves in *U. californica* as compared with *U. speciosa.* Since all three of these Tertiary species show relationship

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to the living white elm, *U. americana* Linnaeus, the trend toward smaller leaf size from the Oligocene to the Pliocene is interpreted as a response to reduced precipitation and summer drought. In parts of eastern North America where there is high summer rainfall, leaves of the white elm are large, like those of the Middle Tertiary *U. speciosa.* Westward, where environments are less humid, this living elm bears leaves whose average size corresponds closely to that of *U. californica* and *U. moragensis.*

In this connection, mention may be made of a tree of *Ulmus americana* now growing beside the highway a few miles east of Mitchell, Oregon, 800 miles west of the natural range of living elms in North America. Rainfall here is not more than 15 inches annually, and native woody plants of the adjacent valley are limited to such typical riparian trees or shrubs as aspen, birch, cherry, cottonwood, and willow. This elm tree must have been planted many years ago, for it has reached a height of approximately 40 feet and a trunk diameter of 3 feet. Its crown is somewhat more globose than is characteristic of the species in the eastern United States, suggesting the shape of trees of *U. pumila* Linnaeus growing along dry washes in Inner Mongolia. Leaves of this Oregon tree reach a length of more than 12.7 cm., but their average length, as based on measurements of 114 leaves from 8 twigs selected from the tree at random, is 7.15 cm. The average length of the fossil leaves of the Troutdale elm is 7.1 cm. It is apparent that the leaves of *U. californica* resemble those of modern elms growing under relatively unfavorable conditions. White elm leaves from several trees in well watered parts of the eastern United States have an average length of 9.0 cm., and correspond closely in size to those of *U. speciosa* from the Miocene of the western United States.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, no. 2601.

Zelkova oregoniana (Knowlton) Brown

Zelkova oregoniana (Knowlton) Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 173, pl. 51, figs. 11–15, 1937.

This genus, now restricted to eastern Asia, is represented by several specimens whose shape and margin readily distinguish them from leaves of *Ulmus.* As was shown in table 32, there are other Pliocene records of *Zelkova oregoniana,* although its occurrence in this epoch is much more restricted than during the Miocene in western North America. The leaves of the modern species *Z. serrata* Makino are closely similar.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2602, 2603, 2604.

Family LAURACEAE

Umbellularia salicifolia (Lesquereux) Axelrod

Umbellularia salicifolia (Lesquereux) Axelrod, Carnegie Inst. Wash. Pub. 516, pp. 102–103, pl. 8, fig. 4, 1939.

Judging from its scant representation in the collections, this species was not a common member of the Pliocene forest of Oregon. It seems possible that it may have been restricted to moist slopes and ravine heads at some distance from sites of deposition, as is the modern California laurel (*Umbellularia californica* Nuttall) in the inner Coast Ranges of California. This would account for the failure of many

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leaves to be buried in the alluvium of the major valleys, where the strictly riparian types are more numerous in the fossil record.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2605, 2606, 2607.

Family HAMAMELIDACEAE

Liquidambar pachyphyllum Knowlton

Liquidambar pachyphyllum Knowlton, U. S. Geol. Surv. Bull. 204, p. 63, pl. 9, fig. 1, 1902. Condit, Carnegie Inst. Wash. Pub. 553, p. 48, pl. 10, fig. 1, 1944 (see synonymy).

A single leaf specimen shows nervation and margin characters which indicate the presence of this Miocene species in northwestern Oregon as late as Pliocene time. Of the living species which have survived in North America and Eurasia, the leaves of *Liquidambar styraciflua* Linnaeus of the eastern United States are most like the Troutdale specimen.

Liquidambar pachyphyllum is a common member of several Miocene floras of Oregon and Washington, including the Lower Miocene Molalla flora from a near-by locality in the Willamette Valley. Specimens referable to this species have recently been collected in the Ellensburg formation of eastern Washington, associated with species which are largely indicative of a xeric environment. This persistence of a few relicts into the Pliocene suggests the local continuance of summer showers, though these must have been much less frequent than during the Miocene, judging from the composition of the Ellensburg and Troutdale floras as a whole.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2608.

Family ROSACEAE

Prunus treasheri new species

(Plate 63, figure 3; plate 64, figure 1)

Description. Leaf ovate-lanceolate, apex acuminate, base rounded and slightly asymmetrical; blade often folded along the midrib so that only one half of the leaf can be seen, in such cases usually somewhat falcate; length 4.5 to 7.0 cm., width 1.5 to 2.4 cm. (estimated), maximum width at about the middle; petiole, where preserved, slender, 9 mm. long; midrib firm, straight in leaves showing both sides of blade, or curved in those showing only one side; secondaries opposite in basal part of leaf, becoming alternate toward the tip, curving, departing at 30° to 50°, looping upward well within the margin; tertiaries widely spaced, angular, forming a series of fine loops along the margin; nervilles forming a small, quadrangular mesh; margin finely serrate; texture medium.

Discussion. The shape of these leaves marks them as different from normal leaves of any living American species, although the leaves of *Prunus serotina* Ehrhart may in some cases be equally slender. *Prunus davidiana* (Carrière) Franchet, the wild peach of north, west, and central China, closely resembles the Troutdale specimens in the shape of its leaves, as does *P. miodavidiana* Hu and Chaney from the Upper Miocene of Shantung (1938, pl. 25, figs. 2, 3).

Prunus treasheri is named in honor of Ray C. Treasher, whose field observations in the lower Willamette Valley have added valuable information regarding the

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Troutdale formation. This species is another example of the well characterized group of Pliocene plants whose modern equivalents are found in Asia.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2609, 2610.

Family LEGUMINOSAE

Amorpha condoni Chaney

(Plate 63, figures 1, 2)

Amorpha condoni Chaney, Carnegie Inst. Wash. Pub. 553, pp. 318–319, pl. 51, figs. 2–4, 1944.

Several detached leaflets seem referable to this species as described in the preceding chapter. Their somewhat larger size is consistent with other indications of a more mesic environment for the Troutdale than for the Dalles flora. If the habit of this plant was similar to that of modern equivalent shrubs such as *Amorpha fruticosa* Linnaeus and *A. californica* Nuttall, it may have been a much more common member of the slope association than its scant representation in Pliocene floras would indicate. Another factor which may have tended to reduce the numbers of leaves and leaflets of legumes in these and earlier Tertiary records is the common dissociation of their leaflets when the plants lose their foliage; the small size of most leaflets makes them relatively inconspicuous, and their commonly thin texture reduces the probability of their preservation after burial.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotypes, nos. 2611, 2612; nos. 2613, 2614.

Family ACERACEAE

Acer sp.

A single fragment is definitely of maple, but is too incomplete to indicate whether it is referable to *Acer glabroides* Brown, a common Miocene species which lasts over into the Pliocene epoch, or to *A. bolanderi* Lesquereux, a characteristic Pliocene species. Either of these may have been present in the Troutdale flora, though judging from the environmental indications of its other members, the Tertiary equivalent of the mountain maple, *A. glabrum* Torrey, seems the more likely.

It is obvious that this specimen has neither stratigraphic nor ecologic significance. Any mention of it is justified only as indicating that the genus was represented in the Troutdale flora.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., no. 2615.

Family RHAMNACEAE

Rhamnus troutdalensis new species

(Plate 64, figures 2, 3)

Description. Leaves rounded ovate to obovate, the base asymmetrical, cordate on one side, shorter and cuneate on the other, the apex twisted and folded in, apparently

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bluntly rounded; length 5.0 to 6.4 cm., width 4.0 to 4.5 cm.; petiole stout, curving, 6 mm. long; midrib heavy, curving; secondaries opposite, craspedodrome or more commonly camptodrome, near the base spreading and extending along the margin, in the distal half of 2 specimens turning in sharply; tertiaries percurrent, branching from the ends of the secondaries to form loops or to enter the teeth; margin coarsely and remotely serrate in the upper half with secondaries or strong tertiary branches ending in the larger teeth; texture subcoriaceous.

Discussion. No previously described species of Tertiary *Rhamnus* shows secondaries curving in at the apex. In this respect two of the Troutdale leaves resemble certain leaves of *R. rugulosus* Hemsley from central and west China, also recorded from Kwangtung in South China. Association of several fragmentary leaves with one of the Troutdale specimens suggests that the mode of attachment may be in clusters at the tips of branchlets, as is the case with *R. rugulosus* (see University of California Herbarium sheets 252241, 252242, 275099, 612179). The leaves of *R. rugulosus* do not have teeth so coarse as those of our specimens, which in this respect differ from any known living or Tertiary species of the genus. It is possible that the larger teeth of the fossils have their size exaggerated by breaking, since the margins are incomplete. The apparently craspedodrome relations of several secondaries with such teeth may also be due to breakage which has removed the ends of looping secondaries. In their shape, nervation, and general aspect, our leaves are so similar to *R. rugulosus* as to suggest that they may have been derived from a common ancestor.

In general aspect these fossil leaves are similar to an undescribed species of *Rhamnus* from the Kincaid Ranch flora near Ashland, which has been correlated with the Bridge Creek flora of the John Day Basin (Chaney, 1938*c*, p. 641); the Ashland leaves, however, are finely serrate, and all the secondaries are spreading.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., cotypes, nos. 2616, 2617.

Family CORNACEAE

Cornus ovalis Lesquereux

(Plate 63, figure 5)

Cornus ovalis Lesquereux, Mem. Harvard Mus. Comp. Zoöl., vol. 6, no. 2, p. 23, pl. 6, figs. 1, 2, 1878.

The occurrence of only a single leaf of this Tertiary equivalent of the creek dogwood, *Cornus californica* C. A. Mey, and of a similar Asiatic species, *C. walteri* Wangerin, is not necessarily an indication of its rarity during the Pliocene. Leaves of shrubs are seldom well represented in the fossil record. In the Dalles flora no leaves of *Cornus* have been recognized, although the floral assemblage is one in which dogwoods might be expected. Sparse representation of this genus in other Tertiary floras of western North America suggests that some other factor than rarity, perhaps the failure of dogwood leaves to be adequately preserved, may be responsible for the small numbers of specimens found.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., plesiotype, nos. 2618, 2618*a* (counterpart); no. 2619.

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Family EBENACEAE

Diospyros andersonae Knowlton

Diospyros andersonae Knowlton, U. S. Geol. Surv. Prof. Paper 140*a*, p. 46, pl. 27, fig. 6, 1926.

Brown, U. S. Geol. Surv. Prof. Paper 186*j*, p. 184, pl. 60, figs. 12–17, 1937.

Several fragmentary leaves have the general size and shape of this species, and their nervation details are definitely indicative of *Diospyros*. Since no differences are apparent between the Troutdale specimens and the figured leaves of the Latah species, and since the latter's survival into the Pliocene is consistent with Tertiary occurrence of associated species, the reference of the specimens to *D. andersonae* seems justifiable in spite of their fragmentary preservation.

Modern Asiatic species whose leaves closely resemble those of *D. andersonae* are *D. kaki* Linnaeus of central China, which is widely cultivated throughout eastern Asia, and *D. lotus* Linnaeus of central and west China. A similar living species in North America is *D. virginiana* Linnaeus.

Occurrence. Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2620, 2620*a* (counterpart).

Family OLEACEAE

Fraxinus caudata Dorf

Fraxinus caudata Dorf (in part), Carnegie Inst. Wash. Pub. 412, I, pp. 106–107, pl. 13, fig. 8 (not figs. 6, 7, which are *Persea coalingensis* (Dorf) Axelrod), 1930.

Several specimens are referable to this species on the basis of their secondaries' looping well within the margins of the leaflets. *Fraxinus oregona* Nuttall, to which this species shows great similarity, is a typically riparian tree whose leaves might be expected to enter the sedimentary record in great numbers. The rarity of the foliage of *Fraxinus* in the fossil record of western North America seems more probably due to some negative factor of preservation than to the rarity of this genus in Tertiary forests.

Occurrence. Buck Creek, loc. 5; Camp Collins, loc. P3922.

Collection. U. C. Mus. Pal., Paleobot. Ser., nos. 2621, 2622 (loc. 5).

INCERTAE SEDIS

Phyllites plinerva new species

(Plate 58, figure 3)

The fossil leaves are too fragmentary to permit definite generic reference. They show a marked resemblance to smaller specimens figured as *Celtis miobungeana* Hu and Chaney (1938, p. 39, pl. 13, figs. 5, 6) from Upper Miocene deposits of northern China, and it is possible that they may be referable to the American Pliocene species *C. kansana* Chaney and Elias. This species occurs in the Ellensburg flora of Washington, of essentially the same age as the Troutdale. These specimens also resemble leaves of *Philadelphus,* although the resemblance is less to those of *P. bendirei* (Knowlton) Chaney than to those of the living *P. lewisii* Pursh. Both *Philadelphus* and *Celtis* are represented in the living riparian vegetation of eastern

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Oregon, and *P. lewisii* is also widely distributed west of the Cascades. Another possible generic reference, if with better material the margin proves to be entire, is *Sassafras*. A species described as *S. hesperia* Berry has been recorded from the Latah formation, and from younger Miocene beds in the Blue Mountains of Oregon. *Sassafras* is now confined to the eastern side of North America. In order to place the Troutdale material on record, the following brief description is added.

Description. Leaves oval, upper quarter missing, base blunt, apparently asymmetrical owing to being torn, actually symmetrical if restored; length preserved 3.2 cm. (4.0 estimated), width 2.4 cm.; midrib firm, slightly curved, basal pair of secondaries leaving midrib at an angle of 30°, curving slightly and reaching upward to about the middle of the blade; upper pair leaving midrib at the middle of the blade, at an angle of 40°; 2 pairs of inconspicuous intersecondaries between the secondaries; tertiaries obscure, forming an angular mesh, apparently looping along the margin; margin entire in lower half, apparently serrate in upper half; texture firm.

Several globose nutlets may be referable to *Celtis*, but their surface markings are not sufficiently well preserved to permit distinction between this genus and *Prunus*.

Occurrence. Buck Creek, loc. 5.

Collection. U. C. Mus. Pal., Paleobot. Ser., holotype, no. 2600.

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PLATES 54—64

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FIG. 1. Locality 5 in the Troutdale formation. Leaf-bearing zone at upper contact of light-colored sandstone.

FIG. 2. Locality 5 in the valley of Buck Creek, showing aspect of modern vegetation

TROUTDALE LOCALITY

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FIG. 1. Lenticular occurrence of gravels in Troutdale formation, near center of Boring Quadrangle.

FIG. 2. Troutdale formation above Fort Collins, locality P3922

TROUTDALE LOCALITY

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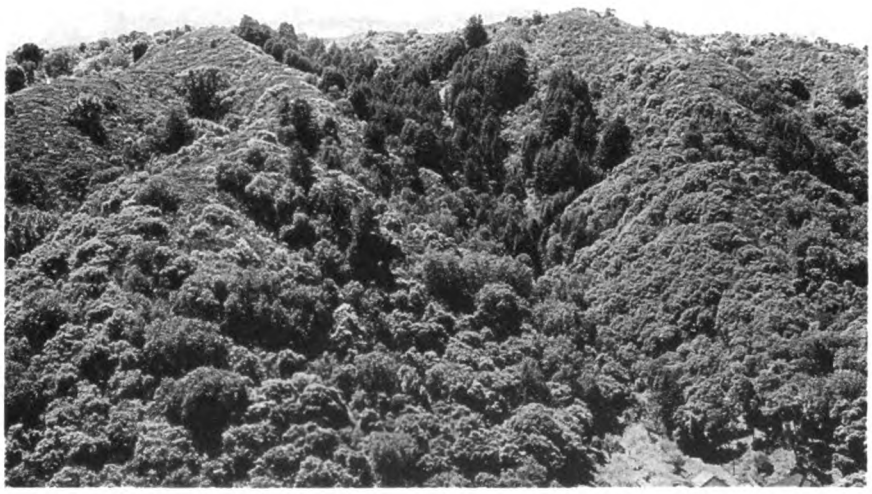

FIG. 1. East face of Berkeley Hills, showing redwoods occupying ravines on oak-covered slopes.

FIG. 2. Valley of Putah Creek 10 miles north of Monticello, California, showing dominant valley oaks on flood plain.

TROUTDALE MODERN EQUIVALENT VEGETATION

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PLATE 57

TROUTDALE FOSSILS

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FIGS. 1, 4. *Cyperacites* sp. U. C. Mus. Pal., Paleobot. Ser., nos. 2587, 2588 . 341

FIG. 2. *Sequoia langsdorfii* (Brongniart) Heer. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2585 340

FIG. 3. *Chamaecyparis gracilis* Condit. Plesiotype. × 2. U. C. Mus. Pal., Paleobot. Ser., no. 2586 340

FIG. 5. *Abies axelrodi* Chaney. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2584 339

FIG. 6. *Pterocarya oregoniana* Chaney. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2593 341

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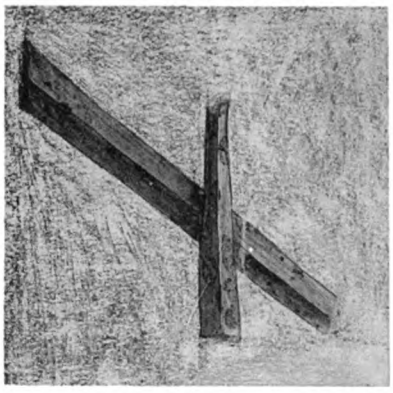

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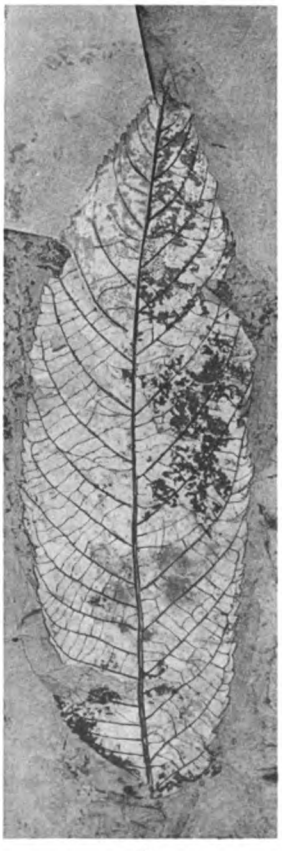

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PLATE 58

TROUTDALE FOSSILS

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FIGS. 1, 4. *Pterocarya oregoniana* Chaney. Paratypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2594, 2595 341

FIG. 2. *Salix wildcatensis* Axelrod. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 1695 341

FIG. 3. *Phyllites plinerva* Chaney. Holotype. U. C. Mus. Pal., Paleobot. Ser., no. 2600 350

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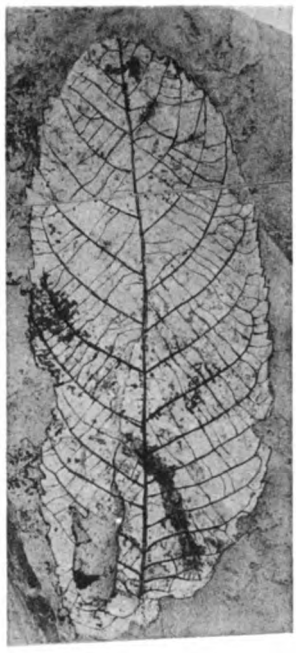

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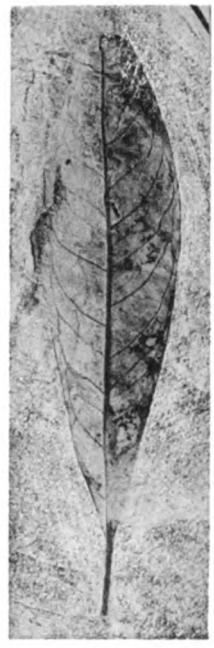

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PLATE 59

TROUTDALE FOSSILS

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FIGS. 1–4. *Salix wildcatensis* Axelrod. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2589, 2590, 2591, 2592 341

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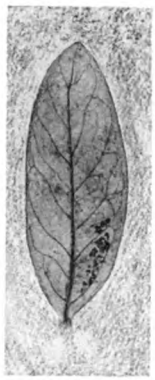

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PLATE 60

TROUTDALE FOSSILS

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FIGS. 1, 3–5. *Quercus winstanleyi* Chaney. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 1690, 2596, 1692, 1693 342

FIG. 2. *Quercus aliena* Blume. U. C. Herbarium sheet 266813. For comparison with *Quercus winstanleyi*.

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PLATE 61

TROUTDALE FOSSILS

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FIGS. 1, 2, 4. *Quercus winstanleyi* Chaney. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2597, 1691, 2599 342

FIG. 3. *Quercus aliena* Blume. U. C. Herbarium sheet 270558. For comparison with *Quercus winstanleyi*.

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PLATE 62

TROUTDALE FOSSILS PAGE

FIG. 1. *Quercus prinus* Linnaeus. × 0.8. U. C. Herbarium sheet 5762. For comparison with *Quercus winstanleyi*.

FIG. 2. *Quercus winstanleyi* Chaney. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 2598 342

FIG. 3. *Quercus fabri* Hance. U. C. Herbarium sheet 356113. For comparison with *Quercus winstanleyi*.

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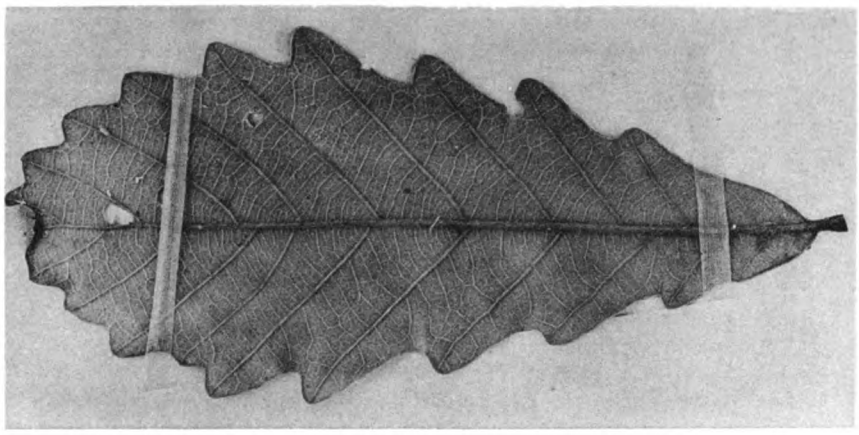

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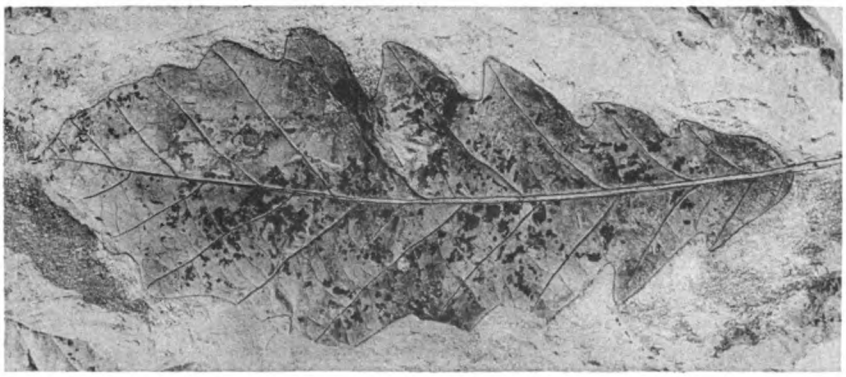

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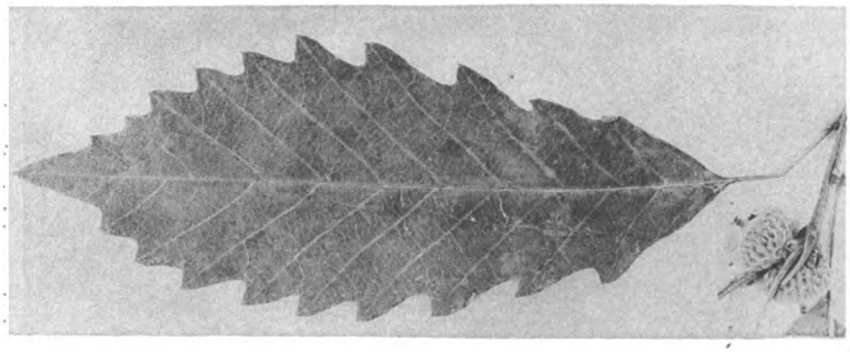

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PLATE 63

TROUTDALE FOSSILS

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FIGS. 1, 2. *Amorpha condoni* Chaney. Plesiotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2611, 2612 348

FIG. 3. *Prunus treasheri* Chaney. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 2609 347

FIG. 4. *Ulmus californica* Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2601 345

FIG. 5. *Cornus ovalis* Lesquereux. Plesiotype. U. C. Mus. Pal., Paleobot. Ser., no. 2618 349

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PLATE 64

TROUTDALE FOSSILS

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FIG. 1. *Prunus treasheri* Chaney. Cotype. U. C. Mus. Pal., Paleobot. Ser., no. 2610 347

FIGS. 2, 3. *Rhamnus troutdalensis* Chaney. Cotypes. U. C. Mus. Pal., Paleobot. Ser., nos. 2616, 2617 348

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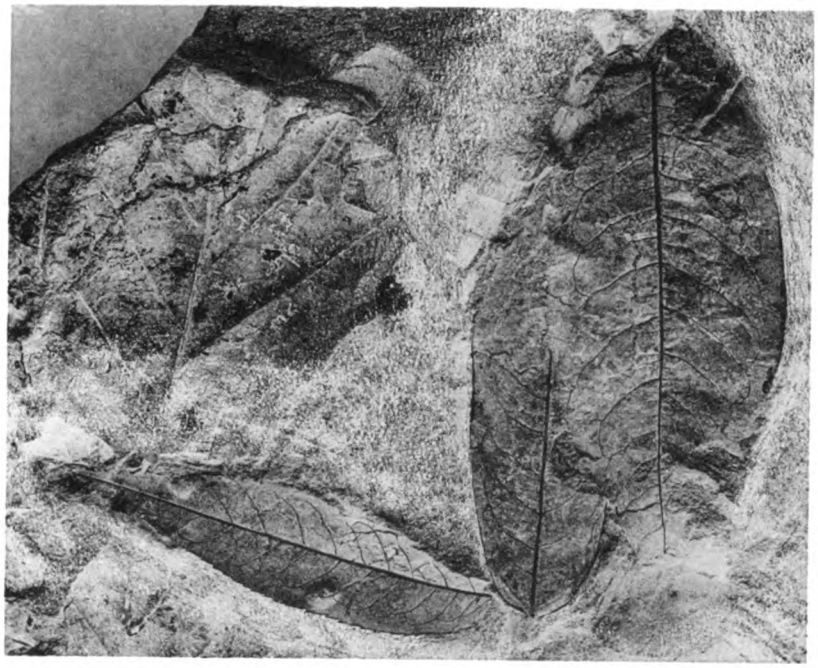

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13

Summary and Conclusions

RALPH W. CHANEY

The preceding chapters have presented detailed information regarding the composition and distribution, both geographic and stratigraphic, of 10 floras ranging in age from transitional Mio-Pliocene to Upper Pliocene. Our final chapter will summarize the relationships of these floras to one another, and to 22 other floras of their approximate age in the western United States.

Table 33 lists 224 fossil species which have been described from the Pliocene of the western United States, and indicates their occurrence at 32 localities ranging in age from transitional Mio-Pliocene to Upper Pliocene. A total of 78 species, representing 34.8 per cent of the total, are known from 8 localities of Middle Pliocene age, of which only 18 are limited to this horizon. There are 90 species known from 10 Lower Pliocene localities, of which only 20 are restricted to beds of that age. From the 10 localities assigned an age transitional between the Pliocene and Miocene, 130 species, representing 58.0 per cent of the total, have been recorded; 30 of these are unknown from other horizons in western North America. From the 4 localities assigned to the Upper Pliocene, 59 species have been collected; all but 26 of these are also known to occur in older horizons of the Pliocene.

Table 33 also shows the occurrence of Pliocene species in 13 Miocene floras. Of these, 70 species have been recorded from the Miocene to the north, where the Arcto-Tertiary Flora[1] was developed, and 33 species from the Miocene to the south, where the Madro-Tertiary Flora[2] had its origin.

The meeting of these two floras in the western United States during the Pliocene epoch has already been discussed, together with the accompanying extinction of many genera of the northern flora, and the survival of identical or modified species from both floras. The details of these extinctions and survivals, and of the areal restrictions of the survivors in post-Miocene time, will be reviewed in the pages which follow.

Interpretation of Tertiary floras in western North America, whether it involves merely the question of their age or the larger consideration of their physical significance in the record of earth history, must depend on an understanding of changes in forest distribution since the Eocene. Movements of the Arcto-Tertiary Flora have been discussed recently by Chaney (Chaney, 1936*a*, 1936*b*; Chaney and Hu, 1940, pp. 103–117 and tables 8, 10), and the migrational history of the Madro-Tertiary Flora has been described by Axelrod (1938; 1939, pp. 47–59; 1940*b*). The progressively southward migration of the northern

[1] See appendix C for list of species.

[2] See appendix D for list of species.

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forest during Tertiary time, and the invasion of much of the western United States by southern woodland vegetation during the latter part of the period, provide a basis for reconstructing topographic changes and climatic trends; at the same time, since such migrations result from physical changes which are a function of time, the successive geographic positions of these floras serve as accurate age indicators of the deposits in which they occur.

As we follow the sequence of floral development down through the Tertiary into Recent time, there is apparent an increasing diversity of vegetation within limited areas. This diversity does not involve greater numbers of species in Pliocene floras, but rather their increasing differentiation into several plant communities. We interpret such differentiation as an expression of a greater variety of habitats, of varied topography resulting from later Tertiary earth movements. First conspicuous in the Pliocene, this diversity of vegetation has persisted down to our day on the western side of an emergent continent. It is in striking contrast with the relative uniformity in composition of the forests from west to east across the state of Oregon during early Tertiary time. Subtropical vegetation, as known from the Comstock and Goshen floras of western Oregon, extended eastward with little change into the John Day Basin, where the Clarno flora represents a forest showing none of the effects of a major topographic and climatic barrier. Even in Middle Tertiary time, the absence of any continuous north-south range corresponding in position and height to the Cascades may be assumed. The Bridge Creek flora of the John Day Basin, of late Oligocene or early Miocene age, contains an abundant representation of redwoods and broad-leafed deciduous trees which indicate a summer-wet climate. The general similarity of this flora to those of the same age in western Oregon, from Kincaid Ranch, Rujada, and Cascadia, has been pointed out, the latter two differing only in their inclusion of a minor element of Caribbean genera which reflect a more coastal environment (Chaney, 1938*c*, pp. 640–644). There is evidence, however, that volcanoes ancestral to at least part of the Cascade Range were exerting a topographic influence on some of the forests of Oregon during Middle Tertiary time; for the Lower Miocene Eagle Creek flora, in coarse sediments which indicate the proximity of great volcanic activity, is characterized by an abundance of black oaks and other slope or upland trees, and has a composition differing greatly from that of the Bridge Creek and other slightly older floras to the south. By later Tertiary time, the influence of the rising Cascade Range is shown by reduced representation of the redwood in such Middle Miocene floras as the Latah of eastern Washington and Idaho, and in the somewhat younger Mascall and equivalent floras of eastern Oregon, Idaho, and Nevada. This range presented only a partial barrier to rain-bearing winds from the west, judging from the survival into these Miocene floras of a considerable number of genera belonging to the East American and East Asian Elements, genera which require regular summer rainfall not available on the Columbia Plateau since the Cascades have attained their present height. As has previously been indicated, the climatic effects of mountain barriers on the vegetation of the

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Pliocene																																
Lower										Middle									Upper													
Dalles	Alvord Creek	Troutdale	Verdi	Esmeralda	Black Hawk Ranch	Diablo	Ricardo	Furnace Creek	Deschutes	Alturas	Oakdale	Petaluma	Mulholland	Anaverde	Mount Eden	Pico	Wildcat	Santa Clara	Sonoma	San Joaquin												
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x		x			x												?															
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western United States are readily apparent at the close of the Miocene and during the Pliocene epoch. Marked differences may be observed in these later Tertiary forests from the Pacific coast eastward to the coastward slopes of the Cascade-Sierra ranges, and across the mountains to the Columbia Plateau and Great Basin.

The wide stratigraphic range of the majority of Pliocene species, with only 82 restricted to any one stage of the epoch, is consistent with the known vertical distribution of many other Tertiary plants on both sides of the Pacific. In our discussion of the stratigraphic ranges of members of the Shanwang flora of northern China (Chaney and Hu, 1940, pp. 103–117), we have considered in some detail the successively later appearance southward of many species of the Arcto-Tertiary Flora. We have now no definite knowledge of a northward migration in Asia corresponding to that of the Madro-Tertiary Flora in North America, but there are evidences of such a southern increment in the Shanwang flora, and the record of its origin and movements will doubtless be apparent when the Tertiary vegetation of eastern Asia has been more fully studied. It seems inevitable that during such broad migrations, either from the north or from the south, there will be some conservative plants which will not be sufficiently modified in their transit over space and time to warrant placing them in new species. Others may be changed to an extent which permits the recognition of distinguishing specific characters. With this concept of the dynamic nature of vegetation, less emphasis is placed on minor or imagined morphological differences, and more on progressively altered distribution throughout the Tertiary period. Migrations under the impetus of changing topography and climate provide a basis for our understanding of the stratigraphic and geographic occurrence of the Pliocene floras discussed in this volume.

The geographic position of Miocene and Pliocene plant localities in western North America has been shown on figure 1 (frontispiece). For convenience in referring to them, the western United States is divided into a northern sector extending from Washington to northern California; a middle sector including the localities of central California and central Nevada; and a southern sector extending from the San Joaquin Valley southward in California. To complete our grid plan of discussion, we are dividing each sector into an interior province, which extends eastward from the Sierra-Cascade summit; a coastward slope province, which includes the western slopes of these mountains and of ranges farther south; and a coast province, which extends inland from the Pacific through the outer Coast Ranges, within the principal zone of marine influence. These nine geographic units present certain natural differences in climate and topography, differences which in many instances extended back into the later Tertiary. Table 34 indicates the distribution of the Mio-Pliocene and Pliocene floras of the western United States by sectors and provinces. Our order of discussion gives first consideration to the oldest flora of the interior province in the northern sector; thereafter we shall consider floras of the same age westward into the coastward slope and coast provinces before going up the

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TABLE 34

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF MIO-PLIOCENE AND PLIOCENE FLORAS IN THE WESTERN UNITED STATES

STAGE	NORTHERN SECTOR			MIDDLE SECTOR			SOUTHERN SECTOR		
	Interior	Coastward slopes	Coast	Interior	Coastward slopes	Coast	Interior	Coastward slopes	Coast
UPPER PLIOCENE			Wildcat			Santa Clara Sonoma		San Joaquin	
MIDDLE PLIOCENE	Deschutes* Alturas				Oakdale	Petaluma Mulholland	Anaverde	Mount Eden	Pico
LOWER PLIOCENE	Ellensburg* Dalles Alvord Cr.	Troutdale		Verdi* Esmeralda		Black Hawk Diablo	Ricardo Furnace Cr.		
MIO-PLIOCENE TRANSITION	Lower Idaho			Fallon* Middle Coal Valley	Mohawk* Forest Remington Hill Table Mtn.	Neroly		Mint Canyon	Upper Puente

*The listing of floras in this space is based on their distribution from north to south, and has no stratigraphic significance.

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stratigraphic column to the succeeding stage of the Pliocene. In the same order from east to west, we shall discuss the floras of the middle and southern sectors in their stratigraphic sequence.

In the Mio-Pliocene transitional flora described by Dorf (1936) and Smith (1938*a*) from southwestern Idaho, there is still a meager occurrence of *Sequoia langsdorfii* and of such broad-leafed deciduous genera as *Ostrya, Ulmus, Ptelea,* and *Cercidiphyllum,* the latter representing one of the most characteristic members of the East Asian Element. *Quercus simulata,* an oak with Asiatic affinities, is the only common member of this Lower Idaho flora which does not have a living equivalent in the western United States. All the other dominant species, falling in such genera as *Acer, Arbutus, Castanopsis, Fraxinus, Juniperus, Mahonia, Platanus, Quercus,* and *Salix,* have living equivalents largely or entirely restricted to the western United States where summer rainfall is greatly reduced. The progressive withdrawal of the redwood and of many broad-leafed deciduous genera from the interior province at the close of the Miocene is interpreted as resulting from a gradually rising topographic and climatic barrier to the west.

By Lower Pliocene time, the East American and East Asian Elements had been further restricted in the interior of the northern sector of the western United States. Of the former there remained in the forest represented by the Dalles flora only the elm, *Ulmus californica,* and the white oak, *Quercus winstanleyi,* both with leaves of reduced size as compared with their Miocene equivalents, *U. speciosa* and *Q. columbiana;* neither of these species is a common member of the Dalles flora. Several other species, such as *Acer negundoides, Cercis buchananensis,* and *Platanus dissecta,* may be considered members of the East American Element, but they also have modern equivalents in the western United States. Members of the Dalles flora which are assignable to the East Asian Element are *Pterocarya oregoniana, Quercus winstanleyi,* and *Ulmus californica,* all sparsely represented. All the typical Miocene species have been eliminated, leaving either modified forms such as the elm and oak above mentioned, or such species as *Acer negundoides, Cercis buchananensis,* and *Salix hesperia,* whose Miocene distribution seems to have been largely marginal, and whose living equivalents are members of riparian communities in regions now semiarid.

Another Lower Pliocene flora, the Alvord Creek from southeastern Oregon, includes three species assigned to the East American Element, *Carpinus grandis, Prunus harneyensis,* and *Rhus alvordensis. Abies alvordensis, Carpinus grandis,* and *Picea sonomensis* are members of the East Asian Element. *Rhus alvordensis* and *Picea sonomensis* are also members of the West American Element. Except for *Rhus alvordensis,* these species make up a minor part of the Alvord Creek flora, and have been interpreted by Axelrod to represent relicts which have survived in topographically favorable situations. A majority of the species, in such genera as *Acer, Amelanchier,* and *Rhus,* are members of the West American Element; their modern equivalents now occupy regions where there are seasonal restrictions in moisture. The Southwest American Element is also

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well represented, indicating the latest northward extension of this unit now recorded, and placing further emphasis on rainfall reduction in the interior.

The only other known flora of Lower Pliocene age from the Columbia Plateau is the Ellensburg of eastern Washington, which may be slightly older and is referred by some workers to the Mio-Pliocene. It is now being studied by the writer in collaboration with George F. Beck; we find such typical Dalles species as *Acer negundoides, Cercis buchananensis, Salix hesperia,* and *Ulmus californica,* all but the last of which have modern riparian equivalents in semiarid parts of the western United States. Associated with them are a few twigs of *Sequoia langsdorfii,* also a sparse representation of *Liquidambar pachyphyllum* and perhaps other members of the East American Element. The significance of such relicts of a more humid stage can be only briefly considered here; they are interpreted as having lasted locally in situations connecting westward with the ocean by broad valleys, or opposite low points in the intervening mountain range. This explanation has been presented for the occurrence of a considerable number of warm-temperate genera in the Miocene Latah and Mascall floras (Chaney, 1938*c*, pp. 644–645). Of similar modern distribution are such conifers as *Abies grandis, Chamaecyparis nootkatensis, Thuja plicata,* and the hemlocks *Tsuga heterophylla* and *T. mertensiana,* which range eastward into Idaho or Montana. All these species have their best development along the Pacific coast, and the eastern limits of their ranges correspond to the occurrence of coastal species in the Ellensburg, Latah, and Missoula floras. In this connection there may be noted the presence of *Castanopsis sonomensis* in the Dalles flora; not only did this species, typically coastal in distribution today, survive east of the growing Cascade Range into the Lower Pliocene, but its modern equivalent, *C. chrysophylla,* has been recorded from near The Dalles. The writer has not noted it there, and it must be supposed that it is rare in this inland position. The chinquapin also occurs as a relict on the west slopes of the central Sierra Nevada.

Direct paleobotanical evidence regarding the age of the Cascade Range is afforded by a comparison between the Dalles flora and the Troutdale flora of the coastward slope. These floras are essentially contemporaneous, but their composition shows that the forests which they represent were living under widely different climatic conditions during the Lower Pliocene. A significant comparison in terms of modern vegetation may be made with the forests of the outer and inner Coast Ranges of California, since these forests contain many of the modern equivalents of the Oregon Pliocene. Westward from the Sacramento Valley to the coast, over a transect shown in text figure 4, the vegetation becomes progressively more mesic in character. The innermost range, known as Blue Ridge, is crossed by Putah Creek, in whose valley (see pl. 50, fig. 1) lives a plant assemblage strikingly similar to the Dalles flora. Box elder is abundant along the stream, together with willow, sycamore, redbud, and grape, all of which are represented by closely similar species in the Dalles flora. On adjacent slopes and extending down to the creek are several species of oak, of which the valley oak, *Quercus lobata,* is most similar to the

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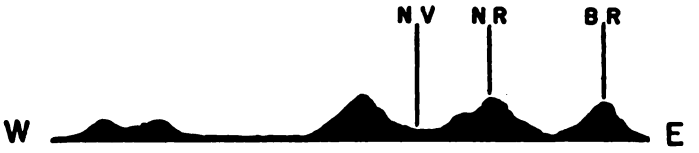
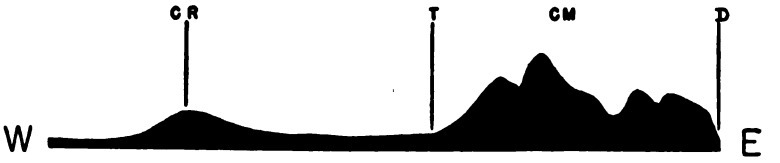
fossil *Q. winstanleyi.* Up the valleys on the east slope of the Napa Range, valley oaks are abundant nearly to the summit. Here rainfall is much increased, and a unique type of vegetation has survived in several deep and narrow valleys (Jepson, 1910, pp. 131–132). This comprises a mixture of such Sierran conifers as *Libocedrus decurrens, Pinus lambertiana,* and *P. ponderosa* with characteristic species of the coast redwood forest, such as *Acer macrophyllum, Cornus nuttallii, Corylus rostrata* var. *californica, Lithocarpus densiflora, Sequoia sempervirens,* and *Umbellularia californica.* Westward down the slope into the Napa Valley, various members of the coast redwood forest occupy sheltered situations in close proximity to the oak woodland of more exposed habitats. The only common member of the Troutdale flora which does not have a modern equivalent in this forest is *Ulmus californica;* it is of interest to note that the modern equivalent species, *U. americana,* grows well under cultivation in this valley and elsewhere in the Coast Ranges of California. The reason for the disappearance of elms from the native vegetation of the western United States is rather difficult to determine in view of its hardiness when planted there. Possibly climatic extremes of the Pleistocene were responsible for its elimination, along with other less resistant genera which characterized the forest of much of the northern hemisphere during Middle Tertiary time; existing climatic barriers have prevented its natural return.

The east-west change in character of modern vegetation from Putah Creek on the inner side of the Coast Ranges to Napa Valley results from the greatly increased precipitation in the valleys nearer the coast. The rainfall at Putah Creek has been estimated (see chap. 11, pp. 297–298) at 22 inches, whereas at stations in Napa Valley to the west it averages 34 inches. This difference in precipita-



Vertical scale: 1 inch=2000 feet
Horizontal scale: 1 inch=20 miles

FIG. 4*a*. Section through the Coast Ranges of California from the Pacific Ocean to the Sacramento Valley, showing the position of Napa Valley (NV), Napa Range (NR), and Blue Ridge (BR).



Vertical scale: 1 inch=2000 feet
Horizontal scale: 1 inch=10 miles

FIG. 4*b*. Section through the Coast Ranges and Cascades of Oregon, showing the position of the Coast Range (CR), the Troutdale localities (T) in the Willamette Valley, the Cascade Mountains (CM), and the Dalles localities (D).

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tion corresponds closely to that which has been estimated for the Troutdale and Dalles floras. With the Cascades at their present height, and in spite of the westward connection of the Columbia River valley, the present difference in rainfall at the Troutdale and Dalles fossil localities is 26 inches. Since the Lower Pliocene difference in rainfall between these two regions was only about 10 inches, as judged from the assumed climatic requirements of the fossil floras, it may be supposed that the intervening mountain barrier was not so high at that time as it is today. This assumption is fully in accord with the opinion of Hodge (1938) and other geologists that the Cascades continued to rise throughout Pliocene and Pleistocene time, and that flows and pyroclastics are still being added. Judging from differences in vegetation on its opposite sides, the height of the Lower Pliocene Cascade Range may have corresponded closely to that of the Napa Range, which now separates the valley of Putah Creek from Napa Valley; this range has an average elevation of 1500 to 1700 feet along its summit. Our comparison of the Dalles and Troutdale floras supports the idea that the Cascades were in an early stage of growth at the beginning of the Pliocene, but only approximate estimates of mountain height can be made on this basis.

Further upbuilding of the Cascade barrier by Middle Pliocene time is indicated by the Deschutes flora of eastern Oregon (Chaney, 1938*a*). There is unfortunately no Middle Pliocene flora known from the west side of the range with which comparisons may be made. But the contrast between the Deschutes and Dalles floras indicates a marked reduction in rainfall during post-Dalles time. The East American and East Asian Elements have not been noted in the Deschutes flora, which is made up largely of aspen, with box elder, cherry, cottonwood, and willow, all members of the West American Element. Vegetation of a similar type is found in eastern Oregon where rainfall is from 14 to 17 inches a year; the Deschutes flora therefore appears to have lived in a climate about 10 inches drier than the Dalles flora. Continued reduction in rainfall since the Deschutes stage is implied by the occurrence of the modern equivalents at elevations 1000 to 1500 feet higher than that of the Deschutes fossil locality; this is consistent with our ideas of continued uplift of the Cascade barrier during post-Deschutes time, and down to the present. No Upper Pliocene floras are known from either the interior or the coastward slope in the northern sector. The present rainfall at the Deschutes fossil locality is 8.5 inches a year, and none of the modern equivalents of the fossil flora are living there.

Another Middle Pliocene flora of the interior, lying to the south on the east side of the Sierra Nevada, is represented by our small collections from near Rattlesnake Butte, just west of Alturas (see chap. 10). Like the Deschutes, the Alturas flora is of a riparian type, but it differs in the dominance of the cottonwood, *Populus alexanderi,* with the aspen, *P. pliotremuloides,* of secondary importance. An elm with greatly reduced leaves, *Ulmus moragensis,* is the only surviving member of the East American Element; the remaining species, poplars and willows, are members of the West American Element. Judging from the occurrence of the modern equivalents of these species, a somewhat

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warmer and drier habitat than the Deschutes seems to be indicated; this is consistent with the position of the Alturas flora more than 200 miles to the south. The estimated annual rainfall of 12 to 15 inches is somewhat lower than that indicated by the Deschutes flora.

No Upper Pliocene floras have been recorded from the interior province of the northern sector, nor from its coastward slopes. The flora from the Wildcat formation of northwestern California has never been fully collected or studied. It includes such genera as *Alnus, Sequoia,* and *Umbellularia,* which are typical members of the Redwood Component of the West American Element; other members of this element are *Fraxinus, Platanus, Populus, Pseudotsuga,* and *Salix.* No typical members of the East American Element are present except a specimen doubtfully referred to *Ulmus; Persea* lingered on from earlier Tertiary time. In contrast with Pliocene floras of the interior province, the Wildcat flora represents a much more mesic assemblage, which is in keeping with its coastal occurrence. It shows close relationship to the modern forest of coastal California, and includes certain species suggesting a somewhat higher average temperature.

In turning to the middle sector, mention may be made of the necessity for considering separately the sequence of floral units in regions with differing latitude or topographic relations. This has been fully discussed by Axelrod in preceding chapters. Such regional consideration of floral development is merely an accentuation of the practice of applying the time-space concept to all interpretations of the age and physical significance of Tertiary vegetation (Chaney, 1936*a*). An especially detailed application of the time-space concept is necessary in the study of Pliocene floras because of the highly diversified character of the environments during this epoch, when extensive orogeny was producing the varied topography and micro-climates which have continued down to the present.

In the middle sector, extending across central California and Nevada, the general pattern of Tertiary history seems to have been the same as at the north, although the Sierra Nevada appears to have been somewhat higher than the Cascades at the beginning of the period. The coarse gravels of the Middle Eocene Ione formation (Allen, 1929, pp. 395–402; MacGinitie, 1941, pp. 7–29) indicate that streams with high gradient flowed down the west slopes of the central Sierra Nevada during the Eocene epoch. Matthes has stated that the Sierra region was a land of moderate altitude with northwestward-trending ridges during the first half of the Tertiary period (1930, p. 28). There seems to have been no such differentiation of vegetation from Pacific coast to Great Basin as there is today. The Chalk Bluffs flora, from the west slope of the central Sierra, is considered by MacGinitie to have "extended eastward, with some modification, as far as the Yellowstone region" (1941, p. 93). Southward from Yellowstone Park, the Green River formation, both in its lithology and in the aspect of at least part of its flora, is definitely indicative of semiarid conditions during Middle Eocene time. As described by Bradley (1930, pp. 88–90), this formation was laid down in intermontane basins which had their origin

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at the close of the Cretaceous. The suggestion that semiarid climate and high relief characterized this region during early Tertiary time has also been made by Blackwelder (1915, pp. 103–112). There is no evidence of similar diversity in topography and climate in the Sierra Nevada region during Eocene or as late as Miocene time. The Lower Miocene Elko flora of eastern Nevada includes *Taxodium* and other mesic genera which suggest a coastal influence on climate and vegetation. But with the close of the Miocene, the evidence of a topographic and climatic barrier is even more striking than that which we have described for the northern sector. The Middle Coal Valley and Fallon floras of western Nevada (Axelrod, unpublished), of an age intermediate between Miocene and Pliocene, represent a woodland association dominated by the Southwest American Element, including such characteristic genera as *Celtis, Juniperus,* and *Quercus.* The Tertiary distribution of this element (termed the Sierra Madrean Element by Axelrod in earlier papers) shows that it was sparingly present during the Miocene as far north as east-central Oregon, where small-leafed oaks occur in the Succor Creek flora. It survived into the Lower Pliocene in the Alvord Creek flora of southeastern Oregon, but thereafter was largely confined to the middle and south sectors. Prominent in the Mio-Pliocene floras of west-central Nevada, the Southwest American Element is associated with survivors of the Arcto-Tertiary Flora, including such genera as *Abies, Amelanchier, Betula, Castanopsis, Pinus, Populus,* and *Ulmus,* all of which are rare.

By contrast, the Mio-Pliocene floras on the coastward slopes of the Sierra Nevada include numerous species of northern origin. This is especially true of the Remington Hill, Forest, and Mohawk floras (see chaps. 2 and 8, and Knowlton, 1911), in which such members of the East American and East Asian Elements as *Berchemia multinervis, Carya egregia, Crataegus newberryi, Liquidambar pachyphyllum, Quercus winstanleyi, Q. pseudo-lyrata,* and *Ulmus californica* have been recorded. *Magnolia dayana* and *Persea pseudo-carolinensis* are members of the Caribbean Element which survived along the coast as relicts of the subtropical Eocene forest, and which extended inland locally. The West American Element is best represented in these floras, including *Sequoia langsdorfii* and *Chamaecyparis gracilis,* whose modern equivalents are largely limited to the coast, and such genera as *Acer, Arbutus, Platanus, Populus, Salix,* and *Umbellularia,* whose equivalent living species range inland. In the Mohawk flora, near the summit of the range, the Southwest American Element has not been noted. Farther south and at a lower elevation, the Remington Hill and Forest floras have a minor representation of this element, including such genera as *Arctostaphylos, Ceanothus, Quercus,* and *Ungnadia,* all of which are rare. The Table Mountain flora (see chap. 3), more southerly and at a still lower altitude, includes fewer members of the West American Element, and a predominant representation of the Southwest American Element, with such typical species as *Quercus convexa* and *Cercocarpus antiquus* abundant, and with many other species whose modern equivalents now live to the south. There are fewer representatives of the East American and East Asian Elements than in the

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adjacent floras at higher altitudes to the north, and *Sequoia* is not recorded. The West American Element, which makes up so prominent a part of the Remington Hill and Forest floras, has here been almost entirely replaced by plants of the Oak woodland Component of the Southwest American Element. Such local variations in Mio-Pliocene vegetation are interpreted as resulting from altitudinal zonation, involving marked differences in climate, with differences in latitude a minor factor.

A coastal flora of transitional Mio-Pliocene age has been described by Condit (1938) from the Neroly formation of the San Pablo group in west-central California. The East American Element is predominant in this flora, with *Taxodium dubium, Nyssa knowltoni,* and other species representing a coastal and river-swamp forest similar to that now found in the southern United States and northward up the Mississippi Valley to southern Illinois and Indiana. An increased number of members of the Caribbean Element is included, as might be expected in a situation bordering the sea; these are *Chionanthus membranaceus, Ilex lomensis, Magnolia californica, Persea pseudo-carolinensis, Smilax diforma,* and *Tetracera castaneaefolia.* Several species are referable to the West American Element, but there is only scant representation of the Southwest American.[8] It is readily apparent from this survey of the Mio-Pliocene floras from the interior to the coast that those in the latter situation have retained many species either identical with or closely related to those of Miocene and older age. Eastward to the west slopes of the Sierra Nevada, these older forms, commonly assigned to the East American and East Asian Elements, and to a lesser extent to the Caribbean Element, are reduced in numbers, and their place is taken by the species of the West American Element; still farther eastward, in the interior province, the Southwest American Element replaces the West American. Today the East American, East Asian, and Caribbean Elements are no longer represented in our coastal forests, and the West American Element is predominant; landward there is increasing representation of the Southwest American Element on the lower coastward slopes of the Sierra and in the interior. We conclude that this forest transect of Mio-Pliocene time corresponds so closely to that of today as to indicate the presence of a major topographic barrier. A progressive trend toward aridity, and increasing summer drought, have resulted in the westward shifting of vegetation during Pliocene and subsequent time, bringing trees to the Pacific coast which earlier lived in the Sierra Nevada, and eliminating those which require summer rainfall.

Lower Pliocene floras of the middle sector are the Esmeralda and Verdi (Upper Truckee) floras, now being studied by Axelrod, who has written preliminary statements regarding them (1940*a*, and unpublished MS). The Esmeralda represents an oak woodland community with associated chaparral, making the Southwest American Element predominant. Microphyllous species of *Mahonia* and *Prunus* suggest the proximity of this woodland to the borders of a desert. The only members of the West American Element are poplars and

[8] A specimen of *Quercus convexa* has been noted by Axelrod in collections from this horizon at the U. S. National Museum.

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Umbellularia, all of which are rare. By contrast, the Verdi flora, lying to the west, suggests forests at higher altitudes and closer to the ancestral Sierra Nevada, where more humid conditions probably prevailed during the Pliocene, as is the case today. The Southwest American Element, with such genera as *Quercus* and *Ceanothus,* is here of minor importance, and the West American Element is well developed. Such genera as *Abies, Castanopsis, Pinus,* and *Populus* are referred to the Sierra-Cascade Component of this element. Both the Verdi flora, and the Esmeralda flora of the drier region to the east of the range, are completely lacking in representatives of the East American and East Asian Elements. Their elimination since the close of the Miocene is considered to have resulted from increasing aridity in Nevada, which was in turn the product of progressive orogeny toward the west.

No Lower Pliocene floras are known from the coastward slopes of the Sierra Nevada. Westward in the vicinity of San Francisco Bay, the Diablo flora (chap. 8) is made up largely of the East American Element, with such genera as *Alnus, Betula, Platanus,* and *Ulmus;* a leaf possibly referable to *Pterocarya* and leaves of *Zelkova* from related beds at a near-by locality would be assigned to the East Asian Element; *Persea pseudo-carolinensis,* one of the most abundant species, falls into the Caribbean Element. The West American Element holds a subordinate position, as in the Neroly flora, with *Umbellularia* and possibly *Platanus* present. No members of the Southwest American Element have as yet been collected; in fact, this flora is known only from small collections which were made by Axelrod in 1942. The Black Hawk Ranch flora (chap. 4) is situated fully 1000 feet above the Diablo in the same section. Its dominant species are *Platanus dissecta, Populus washoensis,* and *Ulmus californica,* all members of the East American Element; these genera have living species which still persist along streams in semiarid regions, although they commonly grow in more humid situations. The importance of this element is in contrast with its rarity or absence in the interior Verdi and Esmeralda floras of the same age. The dominance of the Southwest American Element in these Nevada floras is likewise to be contrasted with its sparse representation in the Black Hawk Ranch (*Cercocarpus, Quercus,* and *Rhus*). As in the case of the Lower Pliocene floras of the interior, the representation of these species which require summer rainfall is greatly diminished as compared with that in the Neroly flora of Mio-Pliocene age.

The Middle Pliocene Oakdale flora from the western borders of the central Sierra Nevada represents an oak savanna and riparian assemblage, including 16 species whose modern equivalents are now found along streams in drier parts of western North America, and on the arid plateaus of northern Mexico and the Southwest (chap. 6). Several genera now regularly found in the chaparral, such as *Arctostaphylos, Ceanothus,* and *Photinia,* are included. These and most of the other genera of the Oakdale flora are assigned to the Southwest American Element. It is the oldest flora from the coastward slope which entirely lacks the East American Element, and may therefore be considered to

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represent the earliest appearance of the modern vegetation which covers the lower slopes of the Sierra.

Middle Pliocene floras of the coastal zone include the Mulholland (chap. 5) and Petaluma (chap. 7). The former is the largest known from the Pliocene of North America, with 43 species represented by 2200 specimens. Like the Oakdale, it represents an oak savanna community with riparian associates, and with the Southwest American Element dominant. In addition to live oaks, *Ceanothus, Celtis, Fremontia, Lyonothamnus, Rhus,* and *Sapindus* are included; there are a number of forms whose modern equivalents are members of the chaparral. All the other elements are sparsely represented; the West American includes *Acer, Alnus, Arbutus, Fraxinus, Populus, Prunus,* and *Umbellularia;* the East American Element is limited to *Berchemia, Nyssa,* and *Populus;* two oaks are the only members of the East Asian Element. The Petaluma flora is similar to the Mulholland, but it is less adequately known. It contains no members of the East Asian Element, and the only member of the East American is the small-leafed elm, *Ulmus moragensis.*

No Upper Pliocene floras are known east of the coastal zone in the middle sector. The Sonoma flora, from north of San Franciso Bay (Dorf, 1930, pp. 37–44; Axelrod, chap. 7), has the West American Element predominant, with members of the Redwood and North-coast coniferous Components most numerous, including *Abies, Alnus, Castanopsis, Lithocarpus, Pseudotsuga, Rhododendron, Sequoia,* and *Tsuga.* Other genera of this element are of border or riparian types, such as *Amorpha, Fraxinus, Platanus,* and *Populus.* The East American Element with *Castanea* and *Ulmus,* and the East Asian with *Mahonia, Quercus,* and *Trapa,* are numerically unimportant, as is the Caribbean Element with *Persea coalingensis.* The Southwest American Element is also rare, including live oaks, *Ceanothus,* and *Photinia,* which probably lived on the exposed borders of the forest. No recent work has been done on the Santa Clara flora, from south of San Francisco Bay, and collections available for study are small (Hannibal, 1911; Dorf, 1930, pp. 52–55). Most of the known species fall into the West American Element, and the representation of the Southwest American Element is small. Neither of the elements from the eastern continental borders is known to be present. It is apparent that before the end of the Pliocene epoch the coastal vegetation of the middle sector had taken on essentially its modern aspect, and it seems probable that the slopes of the Sierra and the central Great Basin were also occupied by plant formations similar in general composition to those of today.

Although Pliocene floras of the southern sector are not included in this volume, it seems desirable to mention here their relations to the later Tertiary vegetation of the middle and northern sectors. Regarding the presence of a Miocene topographic barrier, a comparison between the Middle Miocene Tehachapi flora from the Mohave Desert (Axelrod, 1939) and the Temblor flora from the San Joaquin Valley (*ibid.,* p. 36) indicates that there were greater differences in climate from west to east in southern California than farther

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north. There are no known floras of Mio-Pliocene age in the interior. The Upper Puente flora from the Los Angeles area occurs in beds which have been referred to the Miocene (Chaney, 1921*b*), but the evidence both of the plants and of a tooth of *Hipparion mohavense* (Stock, 1928, pp. 51–53) indicates a position transitional between the Miocene and Pliocene. The Southwest American Element makes up an important part of the Puente flora, including live oaks, *Cercocarpus, Juglans,* and *Lyonothamnus.* Also conspicuous is the Caribbean Element, with *Anona, Ocotea, Persea,* and *Sabal* or *Sabalites.* There is little evidence of the West American Element, and no representation of the East American or East Asian. As compared with the modern vegetation of the south coast of California, the Puente flora indicates a climate considerably warmer and with somewhat higher rainfall.

Eastward to the coastward slopes in the eastern part of the Ventura Basin, the Mint Canyon flora presents the best example in the fossil record of chaparral associated with oak woodland (Axelrod, 1940*c*). *Arctostaphylos, Ceanothus, Cercocarpus, Fremontia,* and *Rhus* form a group which is well represented in our collections. The Oak woodland Component includes *Juglans, Lyonothamnus, Prunus,* and *Robinia,* in addition to several live oaks, and with the Chaparral Component makes up most of the Mint Canyon flora. In his preliminary studies of this flora, Axelrod has noted *Persea* and *Sabal* or *Sabalites* of the Caribbean Element, and *Platanus* and *Populus* of the West American, but they make up a far less conspicuous part of this flora than of vegetation of the same age farther north. Elements from the eastern borders of the continents have not been recorded.

Of the two Lower Pliocene floras, both from the interior, the Furnace Creek includes only a single determinable species, *Lyonothamnus mohavensis* (Axelrod, 1940*d*). The Ricardo flora is better known (Webber, 1933), and appears to represent a desert-border community of oak and palm, with pinyon pine, *Cupressus,* and *Robinia* washed down from sheltered adjacent valleys. A flora recently collected by Axelrod in Anaverde Valley near Palmdale, in the interior, is somewhat younger and may be as young as Middle Pliocene. Plants of the Southwest American Element, such as *Ceanothus, Quercus,* and *Rhus,* are mingled with *Populus pliotremuloides* of the West American, and *Persea coalingensis* of the Caribbean Element. Other Middle Pliocene floras to the west are the Mount Eden and Pico. The former represents a conifer-oak woodland of the coastward slopes, including *Juglans, Pinus,* and *Quercus,* together with the typical chaparral genera (Axelrod, 1937). Aspen and sycamore are members of the West American Element, and *Persea* of the Caribbean, but they are much less conspicuous than the members of the Southwest American Element. The Pico flora is coastal, and is known only from two pine cones (Dorf, 1930, p. 56), which Mason has recently suggested may be related to the living coastal pine, *Pinus torreyana* Parry.

The Upper Pliocene is represented by the San Joaquin flora (Etchegoin of Dorf, 1930, pp. 50–51). It includes such typical members of the Southwest American Element as *Celtis, Garrya,* and *Quercus; Platanus* and *Salix* of the

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West American Element; *Persea* of the Caribbean Element; and a poplar which is referred to the East American Element. Like the Pliocene floras farther north, it is essentially modern in aspect.

In the preceding discussion we have considered Pliocene vegetation in three latitudinal units, the northern, middle, and southern sectors, and have traced its changes along transects from the interior westward to the coastward slopes of the mountains, and on to the Pacific coast. It will be profitable at this point to compare several of the more important floras and floral groups from north to south.

The floras which we have assigned to Mio-Pliocene and Lower Pliocene horizons, hereafter termed "older Pliocene," show a more generalized composition than those from the upper part of the series, hereafter termed "younger Pliocene." When comparisons are made with vegetation now living near the several fossil localities, certain elements which were widely distributed during early Pliocene time are seen to have subsequently disappeared from the western United States. Since their elimination has been progressive, with a gradual introduction of new and surviving elements, a detailed analysis of the composition of Pliocene floras provides an adequate basis for the determination of their relative age, as has been shown by Axelrod in chapter 8.

Older Pliocene floras recorded from the northern and middle sectors include a well marked group of species whose modern equivalents live in regions of summer rainfall, and which we have referred to the East American and East Asian Elements. Best developed at localities on the westward side of the Sierra-Cascade barrier, these elements also have limited representation in the interior. Their widespread occurrence indicates that the climate in this part of western North America was characterized by well distributed precipitation as late as Lower Pliocene time, although on the east side of the mountains there is evidence of considerable summer reduction. Farther south these eastern elements are unrepresented, and members of the Caribbean Element take their place. The genera of this subtropical element, widespread as far north as Washington during the Eocene, might be expected to survive to a later date in southern California than in more northerly regions. Some of them have even lingered on to the present as small trees, shrubs, or vines: *Acacia* spp., *Acalypha californica, Bursera microphylla, Cassia armata, Chilopsis linearis, Diospyros texana, Dodonaea viscosa,* and *Washingtonia filifera* seem to represent survivors of an earlier and warmer stage which have been able to maintain themselves down to the present along the southern border of the western United States.

Although the majority of the broad-leafed deciduous genera of the Arcto-Tertiary Flora also have become extinct in western North America, there have survived in coastward situations or at higher elevations a number of relicts of this temperate, summer-wet forest of earlier Tertiary time. These include species in such genera as *Acer, Alnus, Amelanchier, Cornus, Platanus, Prunus,* and *Quercus* (deciduous species). Their survival has been made possible by reduction in leaf size (in *Populus tremuloides, Prunus demissa, P. emarginata, Quercus lobata*), increased thickness of leaves (*Acer macrophyllum, Quercus*

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garryana, Q. kelloggii, Q. lobata), restriction to the coastal zone of summer fog or to mountain valleys (*Alnus rubra, Cornus nuttallii*), and restriction to stream borders (*Alnus rhombifolia, Cornus pubescens, Prunus demissa, P. emarginata, Platanus racemosa*). *Castanea,* no longer found in western North America, has its modified equivalent in *Castanopsis,* which has small, thick leaves and an evergreen habit. Many conifers of Arcto-Tertiary origin have made similar adjustments in distribution: *Sequoia sempervirens* is confined to the coastal fog belt, and *S. gigantea* to the moist slopes of the Sierra Nevada; *Taxodium mucronatum* is restricted to riparian habitats in Mexico and Guatemala. Such changes in distribution had been only partially effected at the beginning of the Pliocene epoch, judging by the occurrence of members of the East American and East Asian Elements in the Lower Idaho, Ellensburg, Troutdale, and Neroly floras. Stated in terms of elements, the most characteristic major groups of plants of the Tertiary, the East American, East Asian, and Caribbean Elements, survived into the Lower Pliocene with reduced distribution and content, and have subsequently been largely displaced by the West American Element at the north, and by the Southwest American Element at the south.

Though the transitional and Lower Pliocene floras from Washington to central California have in common representation of the East American and East Asian Elements, they show differences which seem to be largely an expression of their range across 9° of latitude. Allowing for their varying position with relation to mountain barriers and their slightly differing age, the Neroly flora of west-central California represents a type of vegetation more warm temperate in aspect than any of the floras to the north. It is the only older Pliocene flora from this general region in which *Magnolia californica, Nyssa knowltoni, Taxodium dubium,* and *Tetracera castaneaefolia* had survived. No coastal floras of this age are known from localities farther north, and comparisons can be made only with the somewhat younger Troutdale flora from the coastward slope of the Cascades in Oregon. The latter is typically temperate, with such conifers as *Abies, Chamaecyparis,* and *Sequoia* taking the place of *Taxodium,* and with *Quercus* and *Ulmus* the predominant angiosperms. If a Mio-Pliocene flora from the coast of Oregon were available for comparison, a closer resemblance to the warm-temperate Neroly forest might be apparent. But in any case this Oregon flora, like the Troutdale flora farther inland, would unquestionably be more typically temperate than that from central California.

A more significant comparison may be made between the Troutdale flora and the Remington Hill from the west slope of the central Sierra. They have in common such typical coastal conifers as *Sequoia langsdorfii* and *Chamaecyparis gracilis,* as well as *Liquidambar pachyphyllum, Quercus winstanleyi, Ulmus californica,* and *Umbellularia salicifolia;* several additional genera are common to the two floras. The East American and East Asian Elements are better represented in the Troutdale, where the Southwest American Element is absent; in the Remington Hill flora, the latter element is only sparingly represented. With these differences in mind, it is still apparent that the coastward

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slopes of the Cascade and Sierra Nevada ranges had forests of a similar type on their more humid slopes during early Pliocene time, a resemblance probably as great as may now be noted between the living forests of Oregon and central California. At lower and drier altitudes, as shown by the Table Mountain flora, the north-south relationship is slight; this more xeric Mio-Pliocene flora shows greater similarity to the Dalles and Ellensburg floras from the northern interior, with which it has in common such riparian species as *Acer negundoides, Celtis kansana, Cercis buchananensis, Platanus dissecta,* and *Ulmus californica.* We may conclude that during early Pliocene time, as today, there was a marked difference in vegetation between the lower slopes and those at middle elevations in the Sierra Nevada. A resemblance comparable with that of living forests of the Transition zone from the Sierra north to the Cascades is indicated by the Remington Hill and Troutdale floras.

Differences between older Pliocene floras are much greater from north to south in the interior than on the coastward slopes. These are consistent with the greater local differentiation noted in modern vegetation at situations where the moderating influences of an adjacent ocean are not operative. As previously stated, the interior floras of Washington, Idaho, and Oregon include species whose modern equivalents occupy regions with summer rainfall, and have a more humid aspect than those in the same province farther south. Such coniferous genera as *Abies, Picea, Pseudotsuga,* and *Sequoia* are restricted to the northern floras, but the more xeric *Juniperus* and *Pinus* are also recorded in Nevada floras. Such typical members of the East American and East Asian Elements as *Cercidiphyllum crenatum, Liquidambar pachyphyllum, Ostrya oregoniana, Ptelea miocenica, Pterocarya oregoniana,* and *Quercus winstanleyi* are unknown in the Nevada floras to the south. But riparian species, *Celtis kansana, Populus alexanderi,* and *Salix truckeana,* range from Nevada to Oregon or Washington, and shrubs such as *Castanopsis perplexa* and *Ceanothus precuneatus* appear to have been widely distributed on the more exposed slopes. Taking the place of the broad-leafed deciduous trees of the northern floras are such Nevada species as *Cercocarpus cuneatus, Mahonia marginata, Prunus moragensis, Quercus hannibali,* and *Q. wislizenoides.* Whereas the northern interior floras represent a valley forest, those to the south are largely riparian, with oak woodland and chaparral species closely associated. The only eastern-element species in common are the wide-ranging *Ulmus californica,* whose living equivalent, *U. americana,* also occupies a great variety of habitats, and an evergreen oak, *Quercus simulata.* Both in the interior and in the coastward-slope provinces, the mesic forests of the north give way to the woodland of the Southwest American Element at the south, with the greatest contrast in the interior. The coastal province at the south has a forest of much warmer aspect than is recorded in any of the older Pliocene floras of Oregon and Washington.

Comparisons between coastal floras of this age from central to southern California show a greater predominance of the Caribbean Element southward. Whereas this element makes up only a subordinate part of the Neroly and Diablo floras, with such genera as *Ilex, Magnolia, Persea,* and *Tetracera,* the

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Upper Puente flora of southern California includes such additional genera as *Anona, Ficus,*[4] *Ocotea,* and *Sabal* or *Sabalites.* A similar contrast is apparent between the forests of the coastward slopes from north to south: the Remington Hill and Table Mountain floras are typically temperate, with the wide-ranging *Persea coalingensis* and *P. pseudo-carolinensis* the only species assignable to the Caribbean Element; the Mint Canyon flora of southern California includes in addition *Diospyros,* a palm, legumes, and others not yet satisfactorily identified. It is clear that latitudinal zoning of vegetation comparable with that of today characterized the older Pliocene floras along the Pacific coast.

Younger Pliocene vegetation is only sparsely represented in western North America. In the northern sector, it is limited to the Wildcat flora of the coast, and the Alturas and Deschutes floras of the interior. There are four coastal floras from the San Francisco Bay area in the middle sector which may be compared with the Wildcat 150 miles to the north. The Mulholland and Petaluma, of Middle Pliocene age, are somewhat older than the others and lived during the driest stage of the Pliocene (see chaps. 5 and 7). They differ from coastal floras of Upper Pliocene age in having a well developed Southwest American Element; oak woodland takes the place of Redwood, Border-redwood, and other components of the West American Element which characterize the Upper Pliocene floras here. The Wildcat flora resembles the Sonoma and Santa Clara floras in its abundance of members of the West American Element. A somewhat higher temperature than that of northwestern California today may be indicated by the occurrence of *Persea pseudo-carolinensis,* although this wide-ranging species may have less significance as a climatic indicator than do living members of this genus which have survived in the region to the south. The absence of live oaks from the Wildcat indicates a somewhat moister and cooler climate than that of central California, where they are well represented in the Sonoma and Santa Clara floras.

No later Pliocene floras are known from the coastward slopes of the northern sector, and the Oakdale flora from the slopes of the central Sierra is the only known younger Pliocene flora from this province in the middle sector. It represents riparian vegetation, with oak woodland and chaparral from adjacent slopes, and differs from the older coastward floras above mentioned in having no representatives of the East American Element. The younger Pliocene vegetation to the north was presumably more humid in aspect on coastward slopes, and may have included survivors from the Miocene, as does the Troutdale, of Lower Pliocene age. In the light of numerous additions to our knowledge of Pliocene floras during the past decade, the discovery of floras to the north may soon provide an adequate basis for completing the sequence of Tertiary vegetation in western Oregon, and in other regions where the record is now inadequate or missing.

In the northern interior, the Deschutes and Alturas floras are entirely West American Element in character with the exception of a small-leafed elm in the Alturas. They have poplars and a willow in common, and indicate vegetation

[4] As yet undescribed.

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like that now living along streams in the vicinity of the fossil localities. No later Pliocene floras are as yet known from Nevada, in the interior of the middle sector. To the south, the little-known Anaverde flora is made up largely of the Southwest American Element, and has only the wide-ranging *Populus pliotremuloides* in common with the floras of the northern interior. This difference is of the order of that between the living vegetation of Oregon and that of southern California. On the coastward slopes, there is greater similarity between the Oakdale flora of the central Sierra and the Mount Eden flora of southern California. Each has a well developed riparian group including *Populus, Salix, Sapindus,* and perhaps *Robinia,* with *Quercus douglasoides* on valley slopes. They differ, as does modern vegetation from central to southern California, in the presence of large-coned pines and desert-border species in the Mount Eden at the south. Southern coastal floras are too meager to permit any significant comparisons with those of central California.

Reference to the Tertiary plant record in eastern Asia indicates changes in distribution and composition corresponding to those described above for western North America. The extended studies of Kryshtofovich in Siberia, and of Yabe, Endo, Miki, and others in Japan, have recently been discussed by the writer (Chaney and Hu, 1940, pp. 103–117) in relation to productive activities of the National Geological Survey of China during the past decade. There is abundant evidence for concluding that reduction in temperature and precipitation corresponding to that in western North America characterized the continental history of eastern Asia during the Tertiary period. Present knowledge does not permit assignment of the Pliocene floras of this region to exact stages, and our present discussion will be confined to a brief review of their composition and geographic distribution.

Coastal floras such as the Hanamaki, Sendai, and Akasi from northeastern to central Honsyu, Japan (Yabe and Endo, 1939, pp. 638–639) have retained the essentially mesic composition of the Miocene and older floras of this region. In fact, the modern forests of Honsyu still bear a strong resemblance to those of middle and later Tertiary age from this region, an indication that climatic conditions have been relatively little altered along the eastern shores of the continent since Miocene time. Except for the elimination of *Sequoia* and reduction in numbers of subtropical genera, the forests living in Honsyu today—even more than those of the eastern United States—seem to resemble the Arcto-Tertiary Flora which migrated southward across the northern continents during the Tertiary period. Pliocene species of *Acer, Alnus, Fagus, Juglans,* and *Ulmus* are referred to the same or to related species in the Miocene, and in some cases have been assigned the modern names of trees living in Japan. A similarly mesic composition characterizes the Ennichi flora of eastern Korea, which may be as young as Lower Pliocene (Kanehara, 1936). The only known Pliocene flora from the eastern United States (Berry, 1916*b*), although perhaps too small to permit far-reaching generalizations, is also made up largely of species which are related on the one hand to the Arcto-Tertiary Flora, on the other to the modern forests of adjacent areas. Apparently there have been less marked

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changes in climate and in vegetation along the eastern coasts of North America and Asia than elsewhere on these continents, with the continuation of summer rainfall from the Miocene down to the present.

Two Pliocene floras have been described from the northern interior of China, the Sanmen from southern Shansi (Chaney, 1935*b*) and the Taiku from the central part of this province (Chaney, 1933). With the exception of fragmentary remains of spruce which appear to have been washed in from adjacent mountains, all the fossils appear to represent trees and shrubs whose living equivalents now occupy riparian habitats in semiarid adjacent areas. Though these Shansi floras are too small to give a complete picture of late Tertiary environments in northern China, the absence from them of the mesic species recorded from the Pliocene of Japan and Korea is consistent with our assumption of seasonal variations in temperature and precipitation. Such species as *Acer pliocenicum, Salix teilhardi,* and *Ulmus shansiensis* closely resemble species described from the Pliocene of the western United States which are considered to have lived in regions of summer drought. Corroborative evidence is furnished by the *Hipparion* clays, which are interpreted by Teilhard as representing fans laid down on the margins of lake basins (1936–1937, p. 198 and map 6). These are widely distributed from China into Mongolia, and both their lithology and their faunas indicate semiarid plains on which trees would be limited to margins of streams.

Still farther inland, the Kucha flora (Chaney, 1935*a*) from Kansu and Sinkiang provinces has an even more xeric aspect, with *Populus norini* the most abundant species at the Tarim Basin locality. The living equivalent of this poplar, *P. euphratica* Olivier, is one of the most widespread riparian trees in the semiarid interior of Asia, extending to northern Africa. The Kucha assemblage, though small, is interpreted as indicating a similar environment, on the basis both of the species represented and of the complete absence of the humid types of Arcto-Tertiary origin. With the Taiku and Sanmen floras farther east, it corresponds in its physical indications to the Deschutes flora from eastern Oregon and the Esmeralda from Nevada, though these American floras are assigned to a position somewhat lower in the Pliocene.

From Yunnan in the southern interior of China, members of the Geological Survey of China have recently obtained small collections of leaves which show relationships to material described from Indo-China and Burma, and have assigned a Pliocene age (Colani, 1917, 1920). Here there is a mingling of such temperate genera as *Betula* and *Quercus* with more numerous subtropical genera, including *Cinnamomum, Ficus,* and members of the Lauraceae. In its general aspect this material from southeastern Asia shows a greater resemblance to the Upper Puente flora of southern California than to other floras from the Pliocene of North America, a similarity consistent with the relatively low latitude of both these floras. The difference in latitude from Sinkiang to Indo-China is about 20°, some 7° more than from central Washington (Ellensburg) to southern California (Upper Puente). On both sides of the Pacific there is evidence

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of marked zoning from middle to low latitudes during the Pliocene, comparable with that of today. There is likewise a marked change in type of vegetation from the coast inland, which is in contrast with the wider ranges of Miocene and older Tertiary floras both in Asia and in North America.

This discussion of the stratigraphic and areal distribution of Pliocene floras, and of their variation in composition from place to place, from stage to stage, may be brought to a conclusion with the following general comments:

1. Later Tertiary vegetation in western North America occupied regions in which topography exerted an influence corresponding to that of today over transects from west to east, and in which latitude had essentially the same control from north to south that it now has. Toward the north, topographic barriers appear to have been much lower at the close of the Miocene than they are today, and a considerable rise in elevation of the Cascade Range during and after Pliocene time is indicated by progressively increasing differences in vegetation from coast to interior. The northern Sierra Nevada, though not affording a climatic barrier at the beginning of the Pliocene as effective as that of today, was sufficiently high to have eliminated most of the genera requiring summer rainfall from its leeward slopes. Lower Pliocene vegetation east of the central Sierra is limited to woodland and chaparral plants, which give way in the southern Sierra Nevada to savanna and desert-border types. It may be concluded that during the Pliocene as today, this range rose to a higher altitude southward.

2. The influence of a climatic trend toward lower temperature and precipitation, temporarily reversed in the Middle Miocene but progressive from the Eocene to the Recent, has resulted in southward and coastward migrations of the Arcto-Tertiary Flora and in the elimination of those elements which require summer rainfall; it has stimulated the northward migration of the Madro-Tertiary Flora, making possible its survival in western North America, especially inland from the coast. Central California and Nevada, lying in a position intermediate between the humid Northwest and the arid plateau of Mexico, have throughout later Tertiary time constituted an ecotonal zone where invading units of vegetation, entering from opposite directions, have mingled on a competitive basis. With progressive desiccation, this competition has restricted descendants of the Arcto-Tertiary Flora to high mountains in the interior, and to humid environments along the coast.

Modern vegetation throughout the western United States is continuing to respond to these physical changes, and its correct interpretation requires not only observation of existing conditions but a reconstruction of later Tertiary environments. An adequate understanding of continental history during the Pliocene, including the nature and extent of topographic change, the climatic trend, and the sequence and dating of events, can only be reached when the fossil plant record is viewed as an earlier phase of forest development which has extended down out of the past, with its latest expression the vegetation of today.

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Appendix A: Systematic Revisions

PAGE

Abies magnifica var. shastensis Lemmon (Mason not Lemmon)=
Abies klamathensis Axelrod 250
Aralia zaddachi ? Heer (Lesquereux not Heer)=
Platanus dissecta Lesquereux 80
Arbutus matthesii Chaney (in part)=
Nyssa elaenoides (Lesquereux) Condit 86
Arbutus matthesii Chaney (Dorf not Chaney)=
Arbutus idahoensis (Knowlton) Brown 262
Betula parce-dentata Lesquereux=
Populus parce-dentata (Lesquereux) Axelrod 129
Castanopsis chrysophylloides Lesquereux (Dorf not Lesquereux)=
Castanopsis sonomensis Axelrod 196
Castanopsis convexa (Lesquereux) Brooks (Dorf, in part, not (Lesquereux) Brooks)=
Quercus hannibali Dorf 199
Celastrus lindgreni Knowlton=
Populus payettensis (Knowlton) Axelrod 253
Crataegus holmesii Lesquereux=
Cercocarpus holmesii (Lesquereux) Axelrod 257
Fagus antipofii Heer (Lesquereux not Heer)=
Quercus bockéei Dorf 76
Ficus mensae Cockerell=
Ficus microphylla Lesquereux 89
Fraxinus caudata Dorf (in part)=
Persea coalingensis (Dorf) Axelrod 132
Heteromeles sp. Dorf=
Photinia sonomensis Axelrod 139
Juglans hesperia Knowlton=
Salix hesperia (Knowlton) Condit 41
Juglans oregoniana Lesquereux (Condit not Lesquereux)=
Salix hesperia (Knowlton) Condit 41
Juniperus sabinoides Ashlee (Dorf not Ashlee)=
Juniperus alvordensis Axelrod 252
Libocedrus dimorpha Oliver (in part)=
Chamaecyparis gracilis Condit 39
Liquidambar acutilobum Chaney=
Liquidambar pachyphyllum Knowlton 48
Liquidambar europaeum patulum Knowlton=
Liquidambar pachyphyllum Knowlton 48
Liquidambar sp. ? Knowlton=
Liquidambar pachyphyllum Knowlton 48

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PAGE

Lithocarpus predensiflora Brooks=
Lithocarpus klamathensis (MacGinitie) Axelrod 197
Myrtus oregonensis Lesquereux=
Quercus convexa Lesquereux 76
Odostemon simplex (Newberry) Cockerell (Berry, in part, not (Newberry) Cockerell)=
Quercus hannibali Dorf 199
Pasania densiflora (Hooker and Arnott) Oersted (Hannibal not (Hooker and Arnott) Oersted)=
Lithocarpus klamathensis (MacGinitie) Axelrod 197
Persea pseudo-carolinensis Lesquereux (in part)=
Magnolia californica Lesquereux 78
Persea sp. Axelrod=
Persea coalingensis (Dorf) Axelrod 132
Philadelphus bendirei (Knowlton) Chaney (Axelrod not (Knowlton) Chaney)=
Philadelphus nevadensis Condit 79
Photinia (Heteromeles) sp. Dorf (Axelrod not Dorf)=
Photinia sonomensis Axelrod 139
Picea lahontense MacGinitie (H. V. Smith not MacGinitie)=
Picea sonomensis Axelrod 191
Picea sp. Brown=
Picea sonomensis Axelrod 190
Pinus sp. Brown=
Picea sonomensis Axelrod 190
Pinus sp. Knowlton=
Picea sonomensis Axelrod 190
Planera myricaefolia (Lesquereux) Cockerell (Knowlton not (Lesquereux) Cockerell)=
Cercocarpus holmesii (Lesquereux) Axelrod 257
Populus alexanderi Dorf (in part)=
Populus prefremontii Dorf 41
Populus dolichophylla H. V. Smith=
Populus payettensis (Knowlton) Axelrod 253
Populus lindgreni Knowlton (Oliver, in part, not Knowlton)=
Populus washoensis Brown 98
Pseudotsuga masoni MacGinitie (Oliver not MacGinitie)=
Picea sonomensis Axelrod 191
Quercus browni Brooks=
Quercus hannibali Dorf 199
Quercus chrysolepis Liebmann (Hannibal not Liebmann)=
Quercus hannibali Dorf 199
Quercus declinata Dorf (in part)=
Quercus hannibali Dorf 199
Quercus elaenoides Lesquereux (in part)=
Quercus convexa Lesquereux 76
Quercus elaenoides Lesquereux (in part)=
Nyssa elaenoides (Lesquereux) Condit 86
Quercus hannibali Dorf (in part)=
Quercus wislizenoides Axelrod 136

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Quercus hannibali Dorf (in part)=
Photinia sonomensis Axelrod 139
Quercus klamathensis MacGinitie=
Lithocarpus klamathensis (MacGinitie) Axelrod 197
Quercus olafseni Heer (Lesquereux not Heer)=
Carya typhinoides (Lesquereux) Condit 75
Quercus orindensis Dorf (in part)=
Quercus douglasoides Axelrod 198
Quercus traini MacGinitie=
Quercus hannibali Dorf 199
Quercus transgressus Lesquereux=
Quercus hannibali Dorf 199
Rhus payettensis Knowlton=
Populus payettensis (Knowlton) Axelrod 253
Rhus typhinoides Lesquereux=
Carya typhinoides (Lesquereux) Condit 75
Salix californica Lesquereux (in part)=
Robinia californica Axelrod 84
Salix coalingensis Dorf (in part)=
Salix hesperia (Knowlton) Condit 41
Salix coalingensis Dorf (in part)=
Persea coalingensis (Dorf) Axelrod 132
Salix coalingensis Dorf (in part)=
Salix vanorensis Axelrod 282
Salix coalingensis Dorf (in part)=
Salix wildcatensis Axelrod 132
Salix florissanti Knowlton and Cockerell (Chaney not Knowlton and Cockerell)=
Salix vanorensis Axelrod 282
Salix inquirenda Knowlton (and previous synonymy, see Brown)=
Salix hesperia (Knowlton) Condit 41
Salix sp. Condit=
Salix hesperia (Knowlton) Condit 41
Salix sp. Dorf=
Sapindus oklahomensis Berry 142
Sapindus lamottei Axelrod=
Sapindus oklahomensis Berry 142
Ulmus affinis Lesquereux=
Ulmus californica Lesquereux 46
Ulmus brownellii Lesquereux (Dorf not Lesquereux)=
Ulmus moragensis Axelrod 283

Additional Synonymy

In assembling table 33, which shows the stratigraphic distribution of transitional Mio-Pliocene and Pliocene species, a few additional errors in identifications and names have been discovered. These include the following:

Cercocarpus antiquus Lesquereux. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 118, 1936=*Fagus washoensis* LaMotte.

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Populus balsamoides Goeppert. Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 248, pl. 55, figs. 3–5, 1883=*Populus emersoni* Condit.

Prunus rustii Knowlton. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 118, pl. 2, fig. 6, 1936=*Prunus chaneyi* Condit.

Thuya garmani Lesquereux. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 109, pl. 1, fig. 1, 1936=*Fokienia* sp.

Wilder is giving a complete discussion of this species in a forthcoming paper on the Lower Miocene Molalla flora of northwestern Oregon. The name to be assigned will be *Fokienia praedecurrens* (Knowlton); this is considered the equivalent of *Libocedrus praedecurrens* Knowlton of the Latah, of *Libocedrus dimorpha* Oliver (in part) of the Blue Mountains, and of *Chamaecyparis gilmoreae* LaMotte of the Upper Cedarville flora.

Ulmus speciosa Newberry. Dorf, Carnegie Inst. Wash. Pub. 476, II, p. 116, 1936=*Ulmus californica* Lesquereux.

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Appendix B: List of Pliocene Species in Elements and Components

In the following lists the West American and Southwest American Elements have been broken down into their various components. The East American, East Asian, and Caribbean Elements have not been so divided, since they have lesser importance in the consideration of the floras described in this volume, and since the details of their component composition have not been adequately worked out.

West American Element

Redwood Component

Alnus rubroides
Castanopsis sonomensis
Chamaecyparis gracilis
Lithocarpus klamathensis
Mahonia hollicki
Myrica sonomensis
Pseudotsuga sonomensis
Pteris calabazensis
Rhododendron sierrae
Salix boisiensis
Sequoia langsdorfii
Umbellularia salicifolia

North-coast coniferous Component

Abies sonomensis
Picea sonomensis
Rhamnus idahoensis
Rhododendron sierrae
Tsuga sonomensis
Vaccinium sonomensis

Sierra-Cascade Component

Abies klamathensis
Acer alvordensis
Amelanchier alvordensis
Amorpha condoni
Castanopsis perplexa
Castanopsis sonomensis
Cercis buchananensis
Chamaebatia prefoliolosa
Mahonia reticulata
Picea sonomensis
Pinus alvordensis
Populus pliotremuloides
Pseudotsuga sonomensis
Rosa alvordensis
Salix payettensis
Salix truckeana
Salix vanorensis
Smilax diforma
Sorbus harneyensis

Border-redwood Component

Acer negundoides
Alnus merriami
Amelanchier alnifolia
Amorpha condoni
Arbutus matthesii
Castanopsis sonomensis
Cercis buchananensis
Chamaecyparis gracilis
Cornus ovalis
Cupressus sonomensis
Fraxinus caudata
Garrya masoni
Juglans pseudomorpha
Philadelphus nevadensis
Pinus pretuberculata
Platanus dissecta
Platanus paucidentata
Populus alexanderi
Populus pliotremuloides
Prunus moragensis
Quercus hannibali
Quercus prelobata
Quercus pseudo-lyrata
Quercus remingtoni

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West American Element—*Continued*

Border-redwood Component—Continued

Rhododendron sierrae
Rhus franciscana
Salix hesperia
Salix wildcatensis
Smilax diforma
Symphoricarpos salmonensis
Umbellularia salicifolia
Viburnum platyspermum

Rocky Mountain Component

Acer bolanderi
Amelanchier alvordensis
Amorpha condoni
Cornus ovalis
Mahonia reticulata
Picea lahontense
Pinus alvordensis
Populus parce-dentata
Populus payettensis
Populus pliotremuloides
Prunus harneyensis
Pseudotsuga sonomensis
Rhus alvordensis
Rosa alvordensis
Salix payettensis
Salix vanorensis
Sorbus harneyensis

Southwest American Element

Oak woodland Component

Ceanothus precuneatus
Celtis kansana
Forestiera buchananensis
Ilex sonomensis
Lyonothamnus mohavensis
Mahonia prelanceolata
Persea coalingensis
Photinia sonomensis
Platanus paucidentata
Populus prefremontii
Prunus petrosperma
Prunus prefasciculata
Quercus convexa
Quercus declinata
Quercus douglasoides
Quercus lakevillensis
Quercus moragensis
Quercus orindensis
Quercus wislizenoides
Ribes mehrtensis
Robinia californica
Salix californica
Salix wildcatensis
Sapindus oklahomensis
Ungnadia clarki

Chaparral Component

Arctostaphylos martzi
Arctostaphylos moragensis
Arctostaphylos oakdalensis
Ceanothus precuneatus
Ceanothus prespinosus
Cercocarpus antiquus
Cercocarpus cuneatus
Cercocarpus holmesii
Dendromecon reticulata
Fremontia lobata
Mahonia malheurensis
Mahonia marginata
Photinia sonomensis
Prunus petrosperma
Quercus dispersa
Rhamnus moragensis
Rhamnus precalifornica
Rhus mensae
Rhus moragensis
Rhus prelaurina

Conifer-woodland Component

Arbutus idahoensis
Juniperus alvordensis

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East American Element

Acer bolanderi
Acer negundoides
Aesculus preglabra
Amorpha condoni
Berchemia multinervis
Carpinus grandis
Carya typhinoides
Castanea pliocenica
Cercis buchananensis
Cornus ovalis
Diospyros andersonae
Ilex opacoides
Juglans pseudomorpha
Liquidambar pachyphyllum
Magnolia californica
Nyssa elaenoides
Persea coalingensis
Persea pseudo-carolinensis
Platanus dissecta
Populus washoensis
Prunus harneyensis
Quercus winstanleyi
Rhus alvordensis
Salix truckeana
Smilax diforma
Ulmus californica
Ulmus moragensis

East Asian Element

Abies alvordensis
Abies axelrodi
Acer negundoides
Carpinus grandis
Cercis buchananensis
Cornus ovalis
Crataegus newberryi
Diospyros andersonae
Mahonia simplex
Picea sonomensis
Prunus treasheri
Pterocarya oregoniana
Quercus bockéei
Quercus simulata
Quercus winstanleyi
Rhamnus troutdalensis
Rhododendron sierrae
Salix wildcatensis
Trapa americana
Ulmus californica
Ulmus moragensis
Zelkova oregoniana

Caribbean Element

Magnolia californica
Persea coalingensis

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Appendix C: List of Pliocene Members of the Arcto-Tertiary Flora

The Arcto-Tertiary Flora is made up of species which are first recorded at high latitudes in deposits largely of Eocene age. By Upper Oligocene and Miocene time, these species or their lineal descendants were members of floras at middle latitudes in North America and Eurasia. Most of the Pliocene members of the Arcto-Tertiary Flora give evidence of a continued southward migration, for they have been recorded in regions still farther south than those occupied by their Middle Tertiary equivalents. Their descendants have survived with little apparent modification in the modern forests of North America, Europe, and northeastern Asia, and many of them have extended their range still farther southward, along mountain ranges into low latitudes.

In the following list of members of the Arcto-Tertiary Flora recorded from the Pliocene of the western United States, there are only two species, *Carpinus grandis* and *Sequoia langsdorfii,* which covered, without observed specific change, the journey south from arctic latitudes. *Alnus rubroides, Castanea pliocenica, Populus alexanderi, Quercus winstanleyi,* and *Zelkova oregoniana* are examples of a considerable group of Pliocene species which are sufficiently different from their Eocene ancestors to warrant the assigning of new specific names; in many cases there are species intermediate in both geographic and phylogenetic position which have been recognized in Upper Oligocene or Miocene floras.

Fully a third of the Pliocene members of the Arcto-Tertiary Flora show no direct relationship to the Eocene members at the north. They are included in this list because they are represented by species of their genera in the older floras at higher latitudes, species which may well have been a part of their ancestral stock. A few Pliocene species are listed as Arcto-Tertiary even though their genera have not yet been recorded from the northern Eocene. The basis for their inclusion is the occurrence of Upper Oligocene or Miocene relatives in Oregon and Washington, and the modern distribution of their living equivalents both in North America and in Eurasia. Species of this last group are marked with an asterisk to distinguish them from members of the Arcto-Tertiary Flora whose ancestors are definitely known to have lived in high northern latitudes during the Eocene epoch.

Abies alvordensis
Abies axelrodi
Abies klamathensis
Abies sonomensis
Acer alvordensis
Acer bolanderi
Acer negundoides
Aesculus preglabra
Alnus merriami
Alnus rubroides
*Amelanchier alvordensis
Amorpha condoni
*Arbutus matthesii
Carpinus grandis

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Carya typhinoides
Castanea pliocenica
*Castanopsis perplexa
*Castanopsis sonomensis
*Cercis buchananensis
*Chamaecyparis gracilis
Cornus ovalis
Crataegus newberryi
Diospyros andersonae
Fraxinus caudata
Ilex opacoides
Juglans pseudomorpha
Liquidambar pachyphyllum
Lithocarpus klamathensis
*Mahonia hollicki
Mahonia simplex
Myrica sonomensis
Nyssa elaenoides
*Philadelphus nevadensis
Picea lahontense
Picea sonomensis
Pinus alvordensis
Pinus pretuberculata
Platanus dissecta
Populus alexanderi
Populus parce-dentata
Populus payettensis
Populus pliotremuloides
Populus washoensis
Prunus harneyensis
Prunus moragensis
Prunus treasheri
*Pseudotsuga sonomensis
Pteris calabazensis
Pterocarya oregoniana
Quercus bockéei
Quercus prelobata
Quercus pseudo-lyrata
Quercus remingtoni
Quercus simulata
Quercus winstanleyi
Rhamnus idahoensis
Rhamnus troutdalensis
Rhododendron sierrae
Rhus alvordensis
Rhus franciscana
Rosa alvordensis
Salix boisiensis
Salix hesperia
Salix payettensis
Salix truckeana
Salix vanorensis
Salix wildcatensis
Sequoia langsdorfii
Smilax diforma
Sorbus harneyensis
*Symphoricarpos salmonensis
Trapa americana
*Tsuga sonomensis
Ulmus californica
Umbellularia salicifolia
Zelkova oregoniana

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Appendix D: List of Pliocene Members of the Madro-Tertiary Flora

The Madro-Tertiary Flora, largely known from recent studies by Axelrod, is first recorded in rocks of Miocene and perhaps of Oligocene age in the southern part of the western United States. The occurrence of many of its species in the central and northern parts of the western United States during the Pliocene is interpreted as indicating a northward migration during later Tertiary time. Many modern equivalents of the Madro-Tertiary species are now living in the western United States and Mexico, with the center of their abundance in the Sierra Madre ranges of Mexico and on adjacent plateaus.

It seems probable that some or all of the species of the Madro-Tertiary Flora had their ultimate origin at the north during Cretaceous or Eocene time. This raises certain questions as to floral assignment which cannot be satisfactorily answered at the present time. *Celtis kansana* and *Ulmus moragensis* are definitely related to the Arcto-Tertiary *Celtis obliquifolia* and *Ulmus speciosa,* and may be considered to be Pliocene derivatives. Their small size and thick texture, however, seem to reflect the more arid conditions at the south under which the Madro-Tertiary Flora is considered to have had its origin. They are included in the following list of Madro-Tertiary species, and are marked with an asterisk to indicate that their ultimate origin may have been at the north.

Arbutus idahoensis
Arctostaphylos martzi
Arctostaphylos moragensis
Arctostaphylos oakdalensis
Ceanothus precuneatus
Ceanothus prespinosus
*Celtis kansana
Cercocarpus antiquus
Cercocarpus cuneatus
Cercocarpus holmesii
Chamaebatia prefoliolosa
Dendromecon reticulata
Forestiera buchananensis
Fremontia lobata
Garrya masoni
Ilex sonomensis
Juniperus alvordensis
Lyonothamnus mohavensis
Mahonia malheurensis
Mahonia marginata
Mahonia prelanceolata
Mahonia reticulata
Photinia sonomensis
Platanus paucidentata
Populus prefremontii
Prunus petrosperma
Prunus prefasciculata
Quercus convexa
Quercus declinata
Quercus dispersa
Quercus douglasoides
Quercus hannibali
Quercus lakevillensis
Quercus moragensis
Quercus orindensis
Quercus wislizenoides
Rhamnus moragensis
Rhamnus precalifornica
Rhus mensae
Rhus moragensis
Rhus prelaurina
Ribes mehrtensis
Robinia californica
Salix californica
Sapindus oklahomensis
*Ulmus moragensis
Ungnadia clarki
Vaccinium sonomensis

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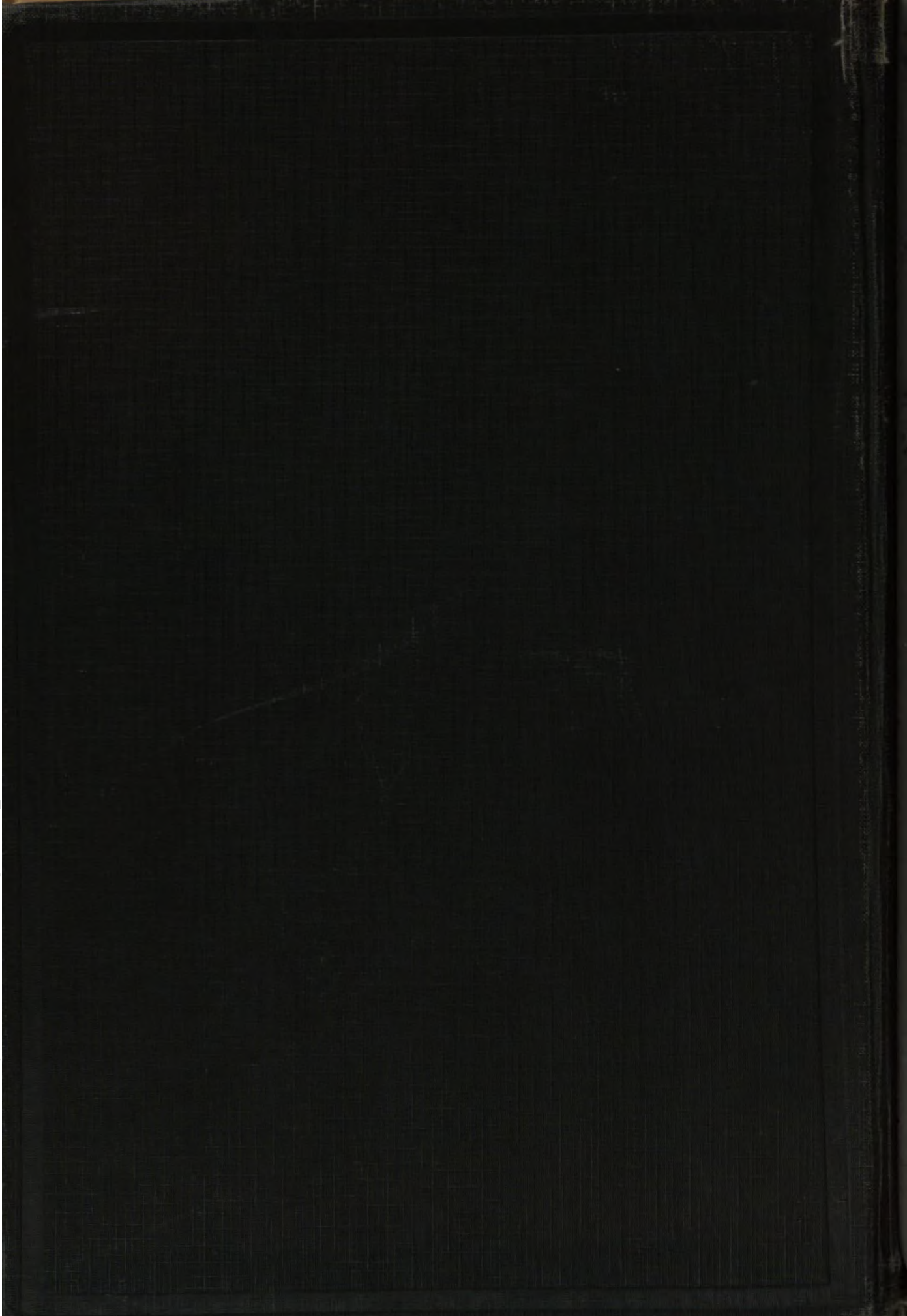

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